A Revision of the Didelphid Marsupial Genus *Marmosa*

Part 2. Species of the Rapposa Group (Subgenus *Micoureus*)

Robert S. Voss, Thomas C. Giarla, Juan F. Díaz-Nieto, and Sharon A. Jansa

Bulletin of the American Museum of Natural History

SHOUT
SHARE
IT

A REVISION OF THE DIDELPHID MARSUPIAL GENUS *MARMOSA* PART 2. SPECIES OF THE RAPPOSA GROUP (SUBGENUS *MICOUREUS*)

ROBERT S. VOSS
Division of Vertebrate Zoology (Mammalogy),
American Museum of Natural History

THOMAS C. GIARLA
Department of Biology,
Siena College, Loudonville, NY

JUAN F. DÍAZ-NIETO
Departamento de Ciencias Biológicas and Grupo de Investigación BEC,
Universidad EAFIT, Medellín, Colombia

SHARON A. JANSA
Department of Ecology, Evolution, and Behavior; and
J.F. Bell Museum of Natural History,
University of Minnesota, St. Paul, MN

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Number 439, 60 pp., 18 figures, 11 tables
Issued June 1, 2020

Copyright © American Museum of Natural History 2020 ISSN 0003-0090

CONTENTS

Abstract 3
Introduction 3
Materials and Methods 4
Molecular Analyses 18
Results 18
Discussion 18
Comparative Morphology 22
Size and External Morphology 22
Craniodental Morphology 25
Taxonomic Accounts 28
The Rapposa Group 28
Marmosa (*Micoureus*) *rapposa* Thomas, 1899 29
Marmosa (*Micoureus*) *parda* Tate, 1931 39
Marmosa (*Micoureus*) *rutteri* Thomas, 1924 42
Acknowledgments 46
References 47
Appendix 1 52
Appendix 2 56
Appendix 3 57

ABSTRACT

In this report, the second of a revisionary series on mouse opossums (*Marmosa*), we analyze cytochrome *b* sequence data from 166 specimens of the subgenus *Micoureus* and delimit putative species using the multirate Poisson Tree Processes (mPTP) method. That analysis identifies 21 putative species, many of which can be matched with available names, including *alstoni*, *constantiae*, *demerarae*, *limae*, *germana*, *meridae*, *paraguayana*, *parda*, *perplexa*, *phaea*, *rapposa*, and *rutteri*. However, some of these nominal taxa are not morphologically diagnosable, and in the absence of other corroborating evidence, we do not recommend that they all be recognized as valid. Phylogenetic analyses of a multigene dataset suggest that putative species of *Micoureus* belong to several well-supported clades, one of which (the "Rapposa Group") is revised in this report. As defined herein, the Rapposa Group includes at least three valid species: *M. rapposa* Thomas, 1899 (including *budini* Thomas, 1920); *M. parda* Tate, 1931; and *M. rutteri* Thomas, 1924. Herein we document their ecogeographic distributions and diagnostic traits, comment on their taxonomic histories, and list the specimens we examined (including all relevant type material).

INTRODUCTION

The didelphid marsupials that Tate (1933) referred to the genus *Marmosa*, Gray, 1821, included many superficially similar small opossums—black-masked, prehensile-tailed, and pouchless—that are now referred to several genera. Of the species that remain in *Marmosa* (sensu Voss et al., 2014), the so-called woolly mouse opossums of the subgenus *Micoureus* have not been revised for many decades, and their taxonomy is correspondingly problematic. Twenty-one available names are currently referred to *Micoureus* (table 1), of which only six (*alstoni*, *constantiae*, *demerarae*, *paraguayana*, *phaea*, and *regina*) were recognized as valid species in the last synoptic treatment of this clade (Gardner and Creighton, 2008). However, recently published molecular and morphological analyses (Silva et al., 2019; Voss et al., 2019) support the recognition of additional valid species and suggest the need for a comprehensive taxonomic revision.

In fact, empirical support for several synonymies implied by current usage is nonexistent. The nominal taxa *germana, mapiriensis*, and *rapposa*, for example, were originally described as full species, and all were regarded as such by Tate (1933) and Cabrera (1958). Although no evidence to the contrary has ever been published, these three taxa are now treated as synonyms or subspecies of *Marmosa regina*. As currently understood, *M. regina* ranges from the Magdalena Valley of Colombia to eastern Bolivia (Gardner and Creighton, 2008: map 35). Because no other small nonvolant mammal is known to be similarly distributed—spanning such formidable barriers as the northern Andes and the upper Amazon—the hypothesis that all the nominal taxa currently synonymized with *M. regina* are conspecific is obviously suspect.

Although phylogenetic analyses of mitochondrial gene sequences have provided useful information about historical relationships among sampled populations of *Micoureus*, analytic results are often difficult to interpret taxonomically in the absence of supporting revisionary work. Patton et al. (2000), for example, discovered that two species with highly divergent cytochrome *b* sequences were broadly sympatric in western Brazil, but the names that properly applied to them were unclear, as the authors themselves acknowledged. A genetically divergent mtDNA haplogroup from southeastern Brazil was successively identified as *M. limae* by Patton et al. (2000), as *M. paraguayana* by Voss et al. (2001), and as *M. travassosi* by Patton and Costa (2003). Confusingly, cytochrome *b* sequences identified as *M. constantiae* have clustered with *M. demerarae* in some studies (e.g., Patton and Costa, 2003), but with *M. regina* in others (e.g., de la Sancha et al., 2012), a paradox that was only recently cleared up by Silva et al. (2019).

TABLE 1

Nominal Species-group Taxa Currently Referred to *Marmosa* (*Micoureus*)

Taxon[a]	Type[b]	Type locality
alstoni Allen, 1900	AMNH 11790/16210	Tres Ríos, Cartago, Costa Rica
arenticola Tate, 1931	AMNH 75691	Arabupu, Bolívar, Venezuela
budini Thomas, 1920	BMNH 20.1.7.134	Altura de Yuto, Jujuy, Argentina
constantiae Thomas, 1904	BMNH 3.7.7.157	Chapada dos Guimarães, Mato Grosso, Brazil
demerarae Thomas, 1905	BMNH 5.11.1.25	Takama, E.D.W.C.B., Guyana[c]
domina Thomas, 1920	BMNH 20.7.14.39	Vila Braga, Pará, Brazil
esmeraldae Tate, 1931	AMNH 76964	Esmeralda, Amazonas, Venezuela
limae Thomas, 1920	BMNH 20.7.14.41	Ceará, Brazil
germana Thomas, 1904	BMNH 80.5.6.77	Sarayacu, Pastaza, Ecuador
mapiriensis Tate, 1931	AMNH 72555	Ticunhuaya, La Paz, Bolivia
meridae Tate, 1931	USNM 137510	"Cafetos de Mérida," Mérida, Venezuela
nicaraguae Thomas, 1905	BMNH 5.10.31.5	Bluefields, S.C.C.A.R., Nicaragua[d]
paraguayana Tate, 1931	BMNH 25.5.1.15	Villa Rica, Guairá, Paraguay
parda Tate, 1931	FMNH 241140	Huachipa, Huánuco, Peru
perplexa Anthony, 1922	AMNH 47188	Punta Santa Ana, Loja, Ecuador
pfrimeri Miranda-Ribeiro, 1936	MN 1245[e]	Rio Palma, Goiás, Brazil
phaea Thomas, 1899	BMNH 98.9.5.2	San Pablo, Nariño, Colombia
rapposa Thomas, 1899	BMNH 98.11.1.13	Huadquiña, Cuzco, Peru[f]
regina Thomas, 1898	BMNH 98.5.15.4	"W Cundinamarca (Bogotá Region)," Colombia
rutteri Thomas, 1924	BMNH 24.2.22.67	Tushemo (near Masisea), Ucayali, Peru
travassosi Miranda-Ribeiro, 1936	MN 1242[e]	Angra dos Reis, Rio de Janeiro, Brazil

[a] Only available names based on Recent material are listed. The gender of names previously combined with *Micoureus* (formerly ranked as a genus, masculine) has been restored to conform with *Marmosa* (feminine).

[b] Holotypes by original designation and examined by R.S.V, except as noted.

[c] The original rendition of this locality was "Comackka, 80 miles up Demerara River, British Guiana" (Thomas, 1905: 314), but this locality (also spelled "Coomacka" or "Kumaka") appears to correspond to the place called Takama in modern gazetteers (e.g., Stephens and Traylor, 1985). E.D.W.C.B. = East Demerara-West Coast Berbice.

[d] S.C.C.A.R. = South Caribbean Coast Autonomous Region.

[e] Lectotype (Langguth et al., 1997); not examined.

[f] Originally "Vilcanota River, just north of Cuzco" (Thomas, 1899b: 43). See species account in this report (below).

With this report, the second in a series on *Marmosa* (Rossi et al., 2010), we initiate a revision of the subgenus *Micoureus* based on analyses of mitochondrial and nuclear gene sequences, first-hand examination of morphological voucher material, and an extensive study of unsequenced specimens, including name-bearing types. Herein we provide a molecular-phylogenetic overview of the subgenus, define several multispecies clades, and formally revise the geographically widespread complex of species closely related to *Marmosa rapposa*, specimens of which have been consistently misidentified in published reports and museum collections for many years.

Materials and Methods

Specimens examined: Specimens cited in our tables and text are preserved in the following collections (listed in order of their standard insti-

tutional abbreviations): AMNH, American Museum of Natural History (New York); BMNH, Natural History Museum (London); CBF, Colección Boliviana de Fauna (La Paz); CM, Carnegie Museum of Natural History (Pittsburgh); CTUA, Colección Teriológica de la Universidad de Antioquia (Medellín); FMNH, Field Museum of Natural History (Chicago); INPA, Instituto Nacional de Pesquisas da Amazônia (Manaus); ISEM, Institut des Sciences de l'Evolution de Montpellier (Montpellier); KU, University of Kansas Biodiversity Research Center (Lawrence); LSUMZ, Louisiana State University Museum of Natural Science (Baton Rouge); MN, Museu Nacional (Rio de Janeiro); MNHN, Muséum National d'Histoire Naturelle (Paris); MUSM, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos (Lima); MSB, Museum of Southwestern Biology (University of New Mexico, Albuquerque); MVZ, Museum of Vertebrate Zoology (University of California, Berkeley); MZUSP, Museu de Zoologia da Universidade de São Paulo (São Paulo); OMNH, Sam Noble Oklahoma Museum of Natural History (Norman); PUCMG, Pontifícia Universidade Católica de Minas Gerais (Belo Horizonte); ROM, Royal Ontario Museum (Toronto); TTU, Museum of Texas Tech University (Lubbock); UFES, Universidade Federal do Espírito Santo); UFMG, Universidade Federal de Minas Gerais (Bello Horizonte); UMMZ, University of Michigan Museum of Zoology (Ann Arbor); and USNM, National Museum of Natural History (Washington, DC). Two specimens with field numbers prefixed by "LHE" have yet to be cataloged in any collection at the time of writing; they are currently held at the USNM.

Taxon sampling and laboratory methods: The cytochrome *b* sequence data analyzed in this report represent most of the nominal taxa currently referred to the subgenus *Micoureus*, including sequences that we obtained from holotypes, paratypes, topotypes, and other geographically representative material (table 2, figs. 1–3). Additionally, we sequenced morphologically distinctive specimens that represent candidate new taxa, and we made a diligent effort to sequence material from sparsely sampled regions. In the latter respect we were not entirely successful, because the eastern slopes of the Andes, much of central Amazonia, southeastern Colombia, and northern Central America are conspicuous sampling gaps.

We also downloaded cytochrome *b* sequence data deposited in GenBank by previous researchers. Careful checking of these sequences for provenance revealed that several pairs of accessions are duplicates (sequences obtained from the same specimen: e.g., AJ606442 and HM106375, both obtained from RSV 2085), of which we retained only the longer sequence from each pair for analysis. We did not analyze the following GenBank accessions, all of which have ambiguous base calls that suggest sequencing problems: AJ606435 (from Steiner and Catzeflis, 2004); GU112916, GU112917, GU112919, GU112921, GU112923, and GU112924 (from Agrizzi et al., 2012); and JN887137 and JN887138 (from de la Sancha et al., 2012). Lastly, we omitted two problematic GenBank sequences (U34673, U34674) for which no satisfactory explanation seems to be available.[1] Other cytochrome *b* sequences were kindly made available to us by the Patton lab at the University of California at Berkeley, of which we discarded four that have premature stop codons (JLP 16758, JLP 16769, JLP 16770, and JLP 16788).

We extracted DNA from preserved tissues or dried museum specimens using methods described in Voss and Jansa (2009) and Giarla et al. (2010). To minimize risk of contamination, all extractions from museum specimens were performed in an isolated laboratory where mamma-

[1] Both sequences are identified in GenBank as "*Micoureus demerarae*," and both were authored by Patton et al. (1996) who, however, listed only a single voucher specimen said to have been collected on the upper Rio Urucu in Amazonas state, Brazil. Unfortunately, neither U34673 nor U34674 appears to be correctly associated with specimens from the Rio Urucu, and their corresponding voucher material is unknown (J.L. Patton, personal commun., 2019). Seemingly anomalous results obtained from phylogenetic analyses of datasets that included U34673 were discussed by Dias et al. (2010), de la Sancha et al. (2012), and Silva et al. (2019).

TABLE 2

Specimens of *Marmosa* (*Micoureus*) Sequenced for Cytochrome *b*

Haplogroup[a]	Voucher[b]	Field #[c]	Locality[d]	bp[e]	GenBank	Source
alstoni	AMNH 139280*	U 3712	Costa Rica: Cartago (70)	978	MN978596	This study
alstoni	KU 143495*	CAL 2830	Costa Rica: Puntarenas (71)	275	MN978597	This study
alstoni	AMNH 131732*	U 3168	Costa Rica: San José (72)	978	MN978598	This study
alstoni	UMMZ 76733*	MJA 34	Nicaragua: Zelaya (87)	372	MN978599	This study
alstoni	USNM 449564*	FMG 2281	Panama: Bocas del Toro (88)	1149	MN978600	This study
alstoni	USNM 449565*	FMG 2293	Panama: Bocas del Toro (88)	1149	MN978601	This study
alstoni	AMNH 272942*	ACC 40	Panama: Colón (89)	475	MN978602	This study
alstoni	FMNH 90097*	KS 24299	Colombia: Chocó (66)	475	MN978603	This study
alstoni	AMNH 148757*		Ecuador: Esmeraldas (73)	275	MN978604	This study
constantiae	AMNH 209158*	AX 2389	Bolivia: Beni (1)	475	MN978605	This study
constantiae	CBF 7540*	EY 1913	Bolivia: Cochabamba (6)	1149	MN978606	This study
constantiae	MSB 57001*	NK 14237	Bolivia: Pando (9)	1149	MN978607	This study
constantiae	USNM 584470*	LHE 1550	Bolivia: Santa Cruz (13)	1149	MN978608	This study
constantiae	[USNM?]	JLS 173	Bolivia: Santa Cruz (14)	630	JF281093	Rocha et al. (2015)
constantiae	[INPA]	MNFS 185	Brazil: Amazonas (18)	1149	MN992047	Patton lab
constantiae	[INPA]	MNFS 187	Brazil: Amazonas (18)	1149	MN992048	Patton lab
constantiae	MVZ 190308	JLP 15833	Brazil: Amazonas (20)	1149	MN978609	This study
constantiae	MVZ 190302	JLP 15368	Brazil: Amazonas (23)	1149	MN978610	This study
constantiae	MVZ 190305	JLP 15632	Brazil: Amazonas (25)	1149	KJ868124	Mitchell et al. (2014)
constantiae	AMNH 92874*	AO 3245	Brazil: Amazonas (26)	372	MN978611	This study
constantiae	OMNH 37209*	MK 0374	Brazil: Mato Grosso (36)	475	MN978612	This study
constantiae	[UFMG?]	LPC 561	Brazil: Mato Grosso (39)	801	JF281084	Rocha et al. (2015)
constantiae	[UFMG?]	LPC 562	Brazil: Mato Grosso (39)	801	JF281085	Rocha et al. (2015)
constantiae	MVZ 197407	LPC 497	Brazil: Mato Grosso (39)	1149	MN978613	This study
constantiae	MVZ 197410	LPC 500	Brazil: Mato Grosso (39)	801	JF281086	Rocha et al. (2015)
constantiae	USNM 544465*	A 1353	Brazil: Pará (48)	475	MN978614	This study
constantiae	USNM 544467*	A 1383	Brazil: Pará (48)	475	MN978615	This study
constantiae	USNM 588015*	LHE 1447	Peru: Cusco (96)	1149	MN978616	This study
constantiae	FMNH 174443*	BDP 4076	Peru: Cusco (97)	1149	MN978617	This study
constantiae	USNM 588018*	MRR 781	Peru: Cusco (98)	1149	MN978618	This study
constantiae	MUSM 15312	DWF 568	Peru: Loreto (105)	802	EF587309	Dias et al. (2010)
constantiae	AMNH 272667*	RSV 2029	Peru: Loreto (105)	1146	HM106374	Gutierrez et al. (2010)
constantiae	MUSM 13294*	RSV 2085	Peru: Loreto (105)	1146	HM106375	Gutierrez et al. (2010)
constantiae	KU 144096*	CAS 715	Peru: Madre de Dios (108)	1149	MN978619	This study
constantiae	FMNH 203510*	BDP 4695	Peru: San Martín (109)	1149	MN978620	This study
demerarae	MN 69110	CRB 2101	Brazil: Amazonas (19)	803	EF587290	Dias et al. (2010)
demerarae	MN 69126	CRB 2178	Brazil: Amazonas (24)	803	EF587291	Dias et al. (2010)

TABLE 2 *continued*

Haplogroup[a]	Voucher[b]	Field #[c]	Locality[d]	bp[e]	GenBank	Source
demerarae	ISEM V-1308	T-2721	French Guiana (77)	800	AJ606437	Steiner & Catzeflis (2004)
demerarae	ISEM V-1320	T-2733	French Guiana (77)	800	AJ606447	Steiner & Catzeflis (2004)
demerarae	ISEM V-966	T-1998	French Guiana (78)	800	AJ606446	Steiner & Catzeflis (2004)
demerarae	ISEM V-973	T-2005	French Guiana (78)	800	AJ606444	Steiner & Catzeflis (2004)
demerarae	ISEM V-972	T-2006	French Guiana (78)	820	AJ487005	Steiner & Catzeflis (2004)
demerarae	ISEM V-884*	T-2083	French Guiana (78)	1149	MN978621	This study
demerarae	ISEM V-1040	T-2287	French Guiana (78)	796	AJ606440	Steiner & Catzeflis (2004)
demerarae	ISEM V-1590	T-3615	French Guiana (79)	799	AJ606436	Steiner & Catzeflis (2004)
demerarae	ISEM V-1183	T-2468	French Guiana (80)	659	AJ606439	Steiner & Catzeflis (2004)
demerarae	ISEM V-1143	T-2526	French Guiana (81)	787	AJ606438	Steiner & Catzeflis (2004)
demerarae	ROM 104708*	F 38299	Guyana: Potaro-Siparuni (82)	799	AJ606434	Steiner & Catzeflis (2004)
demerarae	KU 154874*	F 39096	Guyana: Potaro-Siparuni (83)	1149	MN978622	This study
demerarae	ROM 113431*	F 50411	Guyana: U.Demerara-Berbice (84)	1149	MN978623	This study
demerarae	ROM 106634*	F 38631	Guyana: U.Takutu-U.Esse-quibo (85)	1149	MN978624	This study
demerarae	ROM 98124	FN 31126	Guyana: U.Takutu-U.Esse-quibo (86)	800	AJ606441	Steiner & Catzeflis (2004)
demerarae	USNM 560533	ALG 14086	Venezuela: Amazonas (110)	801	JF281070	Rocha et al. (2015)
demerarae	USNM 560731*	ALG 14485	Venezuela: Amazonas (111)	1149	U34674	Patton et al. (1996)
demerarae	USNM 560741*	ALG 14656	Venezuela: Amazonas (112)	1149	MN978625	This study
demerarae	MVZ 160041*	JLP 9046	Venezuela: Bolívar (114)	726	MN978626	This study
germana A	ROM 105521*	F 37754	Ecuador: Orellana (76)	1149	MN978627	This study
germana A	TTU 98988*	TK 73900	Peru: Loreto (103)	1149	MN978628	This study
germana A	TTU 101236*	TK 75120	Peru: Loreto (103)	1149	MN978629	This study
germana A	KU 157972*	RMT 4053	Peru: Loreto (106)	1149	MN978630	This study
germana A	KU 157973*	NW 855	Peru: Loreto (107)	1149	MN978631	This study
germana B	LSUMZ 28018*	JMC 243	Peru: Loreto (104)	1149	MN978632	This study
limae A	[UFMG?]	LPC 446	Brazil: Mato Grosso (37)	801	GU112918	Agrizzi et al. (2012)
limae A	MVZ 197415	LPC 748	Brazil: Mato Grosso (38)	1149	MN978633	This study
limae A	[MN?]	CRB 2791	Brazil: Mato Grosso (40)	803	EF587295	Dias et al. (2010)
limae A	USNM 549286*	MDC 598	Brazil: Pará (47)	1149	MN978634	This study

TABLE 2 *continued*

Haplogroup[a]	Voucher[b]	Field #[c]	Locality[d]	bp[e]	GenBank	Source
limae A	USNM 549287*	MDC 602	Brazil: Pará (47)	1149	MN978635	This study
limae A		BAC 313	Brazil: Pará (49)	801	JF281079	Rocha et al. (2015)
limae A		BAC 352	Brazil: Pará (49)	801	JF281073	Rocha et al. (2015)
limae A	[uncataloged]*	TL 17107	Brazil: Pará (51)	726	MN978636	This study
limae A		RNL 88	Brazil: Pará (52)	801	JF281090	Rocha et al. (2015)
limae A		RNL 89	Brazil: Pará (52)	801	JF281076	Rocha et al. (2015)
limae A		RGR 537	Brazil: Pará (53)	801	JF281075	Rocha et al. (2015)
limae A		RGR 32	Brazil: Tocantins (57)	801	JF281078	Rocha et al. (2015)
limae A		RGR 34	Brazil: Tocantins (57)	801	JF281077	Rocha et al. (2015)
limae A		RGR 360	Brazil: Tocantins (57)	801	JF281072	Rocha et al. (2015)
limae A		RGR 549	Brazil: Tocantins (58)	801	JF281092	Rocha et al. (2015)
limae A		RGR 148	Brazil: Tocantins (59)	801	JF281071	Rocha et al. (2015)
limae B	BMNH 20.7.14.41*		Brazil: Ceará (34)	498	MN978637	This study
limae B	[MN?]	CRB 2304	Brazil: Goiás (35)	803	EF587292	Dias et al. (2010)
limae B	MN 67083	CRB 2320	Brazil: Goiás (35)	803	EF587293	Dias et al. (2010)
limae B	[MN?]	CRB 2324	Brazil: Goiás (35)	803	EF587294	Dias et al. (2010)
limae B		RNL 100	Brazil: Pará (50)	801	JF281088	Rocha et al. (2015)
limae B		RNL 103	Brazil: Pará (50)	801	JF281089	Rocha et al. (2015)
limae C	[UFES?]	LPC 898	Brazil: Alagoas (17)	801	JF281091	Rocha et al. (2015)
limae D	[UFMG?]	LPC 106	Brazil: Bahia (27)	801	JF281082	Rocha et al. (2015)
limae D	MVZ 197416*	LPC 198	Brazil: Bahia (28)	1149	MN978638	This study
limae D	MVZ 197417*	LPC 199	Brazil: Bahia (28)	1149	MN978639	This study
limae D	MVZ 197419*	LPC 209	Brazil: Bahia (28)	801	GU112915	Agrizzi et al. (2012)
limae D	[UFMG?]	LPC 222	Brazil: Bahia (28)	801	JF281080	Rocha et al. (2015)
limae D	[UFMG?]	LPC 229	Brazil: Bahia (28)	801	JF281081	Rocha et al. (2015)
limae D	[UFMG?]	RM 108	Brazil: Bahia (29)	803	EF587299	Dias et al. (2010)
limae D	[UFMG?]	RM 109	Brazil: Bahia (29)	803	EF587297	Dias et al. (2010)
limae D	[UFMG?]	RM 198	Brazil: Bahia (30)	803	EF587300	Dias et al. (2010)
limae D		SLF 13	Brazil: Bahia (31)	801	JF281083	Rocha et al. (2015)
limae D	[UFMG?]	RM 219	Brazil: Bahia (32)	803	EF587296	Dias et al. (2010)
limae D	[UFMG?]	RM 116	Brazil: Bahia (33)	803	EF587298	Dias et al. (2010)
meridae	USNM 280895*	PH 1132	Colombia: Cesar (65)	1149	MN978640	This study
meridae	USNM 280896*	PH 1180	Colombia: Cesar (65)	475	MN978641	This study
meridae	AMNH 276581*	RPA 312	Venezuela: Falcón (115)	1149	MN978642	This study
paraguay-ana A		YL 81	Brazil: Minas Gerais (42)	801	JF281068	Rocha et al. (2015)
paraguay-ana A	MVZ 197594	YL 92	Brazil: Minas Gerais (42)	801	JF281069	Rocha et al. (2015)

TABLE 2 *continued*

Haplogroup[a]	Voucher[b]	Field #[c]	Locality[d]	bp[e]	GenBank	Source
paraguayana A	[PUCMG?]	JEQ 01	Brazil: Minas Gerais (43)	803	EF587303	Dias et al. (2010)
paraguayana A	[PUCMG?]	CB 01	Brazil: Minas Gerais (44)	803	EF587307	Dias et al. (2010)
paraguayana A		YL 75	Brazil: Minas Gerais (45)	801	GU112920	Agrizzi et al. (2012)
paraguayana A	MVZ 197593	YL 76	Brazil: Minas Gerais (45)	1149	MN978643	This study
paraguayana A	[UFMG?]	266	Brazil: Minas Gerais (46)	801	EF587288	Dias et al. (2010)
paraguayana A	[UFMG?]	A 1091	Brazil: Minas Gerais (46)	803	EF587301	Dias et al. (2010)
paraguayana A	[UFMG?]	A 1427	Brazil: Minas Gerais (46)	803	EF587302	Dias et al. (2010)
paraguayana A	[UFMG?]	A 890	Brazil: Minas Gerais (46)	803	EF587308	Dias et al. (2010)
paraguayana A	[UFMG?]	A 1317	Brazil: Minas Gerais (46)	803	EF587304	Dias et al. (2010)
paraguayana A	[UFMG?]	A 1421	Brazil: Minas Gerais (46)	803	EF587306	Dias et al. (2010)
paraguayana A	[UFMG?]	A 315	Brazil: Minas Gerais (46)	803	EF587305	Dias et al. (2010)
paraguayana A		LPC 792	Brazil: São Paulo (56)	801	GU112922	Agrizzi et al. (2012)
paraguayana A		TK 129697	Paraguay: Canindeyú (91)	801	JN887140	de la Sancha et al (2012)
paraguayana A		TK 129479	Paraguay: Itapúa (92)	801	JN887139	de la Sancha et al (2012)
paraguayana B	MN 46888	CRB 1287	Brazil: Rio de Janeiro (54)	803	EF587289	Dias et al. (2010)
paraguayana B	MVZ 182064*	MAM 46	Brazil: São Paulo (55)	1146	HM106372	Gutierrez et al. (2010)
paraguayana B	MVZ 182065*	MAM 47	Brazil: São Paulo (55)	1146	HM106373	Gutierrez et al. (2010)
paraguayana B	MZUSP 29195		Brazil: São Paulo (55)	630	JN887141	de la Sancha et al (2012)
parda	FMNH 24139*	EH 6493	Peru: Huánuco (100)	475	MN978644	This study
perplexa	USNM 513425*	ALG 13224	Ecuador: Loja (74)	475	MN978645	This study
perplexa	UMMZ 176563*	LLW 1066	Peru: Cajamarca (95)	1149	MN978646	This study
phaea	INPA 2514	VCSV 61	Brazil: Amazonas (21)	630	MN992049	Patton lab
phaea	INPA 2515	VCSV 65	Brazil: Amazonas (21)	630	MN992050	Patton lab
phaea	CTUA 495	JFD 109	Colombia: Antioquia (60)	1149	MN978647	This study
phaea	CTUA 497	JFD 111	Colombia: Antioquia (60)	1149	MN978648	This study

TABLE 2 *continued*

Haplogroup[a]	Voucher[b]	Field #[c]	Locality[d]	bp[e]	GenBank	Source
phaea	FMNH 69863*	PH 3764	Colombia: Antioquia (61)	475	MN978649	This study
phaea	FMNH 69866*	PH 4747	Colombia: Antioquia (62)	726	MN978650	This study
phaea	FMNH 88543*	KS 23068	Colombia: Cauca (64)	1149	MN978651	This study
phaea	FMNH 70915*	PH 5281	Colombia: Huila (67)	978	MN978652	This study
phaea	FMNH 70911*	PH 5320	Colombia: Huila (67)	475	MN978653	This study
phaea	FMNH 70922*	PH 5389	Colombia: Huila (68)	978	MN978654	This study
phaea	FMNH 70923*	PH 5381	Colombia: Huila (69)	978	MN978655	This study
phaea	AMNH 277739*	EEG 136	Venezuela: Aragua (113)	1149	MN978656	This study
phaea	AMNH 277729*	RPA 341	Venezuela: Aragua (113)	1149	MN978657	This study
rapposa A	BMNH 98.11.6.13*		Peru: Cuzco (99)	498	MN978658	This study
rapposa B	[USNM]*	LHE 1307	Bolivia: Chuquisaca (2)	1149	MN978659	This study
rapposa B	[USNM]*	LHE 1299	Bolivia: Chuquisaca (3)	1149	MN978660	This study
rapposa B	MSB 63277*	NK 21697	Bolivia: Chuquisaca (4)	1149	MN978661	This study
rapposa B	AMNH 264924*	NK 30312	Bolivia: Cochabamba (5)	1149	MN978662	This study
rapposa B	CBF 7556*	EY 1917	Bolivia: Cochabamba (6)	1149	MN978663	This study
rapposa B	CBF 7551*	FGS 03-15	Bolivia: Cochabamba (6)	1149	MN978664	This study
rapposa B	TTU 34785*	WDW 967	Bolivia: La Paz (7)	498	MN978665	This study
rapposa B	AMNH 275463*	NK 25648	Bolivia: La Paz (8)	1149	MN978666	This study
rapposa B	AMNH 275464*	NK 25729	Bolivia: La Paz (8)	1149	MN978667	This study
rapposa B	MSB 67019*	NK 22792	Bolivia: Santa Cruz (10)	1149	MN978668	This study
rapposa B	MSB 59883*	NK 15501	Bolivia: Santa Cruz (11)	1146	HM106368	Gutierrez et al. (2010)
rapposa B	AMNH 275466*	NK 23272	Bolivia: Santa Cruz (12)	1146	HM106369	Gutierrez et al. (2010)
rapposa B	MSB 87093*	NK 23983	Bolivia: Tarija (15)	1149	MN978669	This study
rapposa B	USNM 390023*	MLK 12192	Brazil: Mato Grosso do Sul (41)	475	MN978670	This study
rapposa B	MSB 67000*	NK 22521	Paraguay: Amambay (90)	1149	MN978671	This study
rapposa B	UMMZ 174909*	GD 377	Paraguay: San Pedro (93)	1149	MN978672	This study
rapposa B	UMMZ 174992*	GD 387	Paraguay: San Pedro (93)	384	MN978673	This study
rapposa C	USNM 582111*	LHE 1388	Peru: Junín (101)	1149	MN978674	This study
rapposa C	USNM 582112*	LHE 1396	Peru: Junín (101)	1149	MN978675	This study
rutteri	MVZ 190332*	MNFS 1232	Brazil: Acre (16)	1149	MN992051	This study
rutteri	MVZ 190323*	JLP 15435	Brazil: Amazonas (22)	1146	HM106370	Gutierrez et al. (2010)
rutteri	MVZ 190324*	JLP 15436	Brazil: Amazonas (22)	630	JN887142	de la Sancha et al (2012)
rutteri	FMNH 70966*	PH 5913	Colombia: Caquetá (63)	475	MN978676	This study
rutteri	MVZ 154766*	JLP 7745	Peru: Amazonas (94)	1149	U34675	Patton et al. (1996)
rutteri	AMNH 273164*	DWF 659	Peru: Loreto (105)	1149	MN978677	This study
rutteri	KU 144095*	NW 505	Peru: Madre de Dios (108)	1149	MN978678	This study

TABLE 2 *continued*

Haplogroup[a]	Voucher[b]	Field #[c]	Locality[d]	bp[e]	GenBank	Source
"Yasuni"	ROM 118880*	F 41891	Ecuador: Orellana (75)	1149	MN978679	This study
"Yasuni"	KU 157974*	RMT 4088	Peru: Loreto (102)	1149	MN978680	This study
"Yasuni"	TTU 99000*	TK 73966	Peru: Loreto (103)	1149	MN978681	This study

[a] Putative species as delimited by mPTP (see text).
[b] Asterisks indicate specimens examined by the authors. Square brackets enclose the assumed or conjectured repositories of uncataloged material or specimens for which we were unable to determine catalog numbers.
[c] Used to label terminals in figures 1–3. Some sequences obtained from morphological specimens lack entries in this column.
[d] Country and next-largest administrative unit (state, department, province, etc). Numbers in parentheses refer to gazetteer entries (appendix 1), which provide additional geographic information.
[e] Number of sequenced base pairs of cytochrome *b*.

lian polymerase chain reaction (PCR) products were not present. We PCR-amplified the mitochondrial gene cytochrome *b* (CYTB), intron 14 of the X-linked gene encoding O-linked N-acetylglucosamine transferase (OGT), and four autosomal loci (breast cancer activating gene 1 exon 11 [BRCA1], interphotoreceptor retinoid-binding protein exon 1 [IRBP], solute carrier family 38 intron 7 [SLC38], and an anonymous noncoding locus [Anon128]) using the primers and methods described in Voss and Jansa (2009), Giarla et al. (2010, 2014), Gutiérrez et al. (2010), and Pavan et al. (2014). Primers used to amplify cytochrome *b* from degraded DNA extracted from dried tissue are listed in appendix 2. The resulting PCR products were Sanger-sequenced on an ABI 3730xl automated sequencer.

MOLECULAR DATA ANALYSIS: The cytochrome *b* sequences we analyzed are listed in table 2 and the nuclear gene sequences are listed in table 3. All sequences were edited and assembled in Geneious Pro version 7.0 (http://www.geneious.com, Kearse et al., 2012); length heterozygotes in the nuclear loci were resolved using Indelligent version 1.2 (Dmitriev and Rakitov, 2008). Individual genes were aligned using the default parameters of MUSCLE (Edgar, 2004), and alignments of all protein-coding loci were examined with reference to translated amino-acid sequences.

We estimated a maximum-likelihood (ML) cytochrome *b* phylogeny in IQ-TREE 1.6.11 (Nguyen et al., 2014) using IQ-TREE's built-in substitution model testing (Kalyaanamoorthy et al., 2017) and partitioning capabilities (Chernomor et al., 2016) to simultaneously estimate the tree and the best-fitting model for each codon position. We evaluated nodal support using 1000 ultrafast bootstrap replicates (the UFBoot2 algorithm; Hoang et al., 2017). All other settings were left at their default values.

We obtained putative species delimitations from the CYTB tree using the multirate Poisson Tree Processes method (mPTP; Kapli et al., 2017). This approach accounts for differences in coalescent rates among lineages and has a Markov Chain Monte Carlo (MCMC) sampling method for assigning an average support value to each ML delimitation. Within mPTP, we estimated the minimum branch-length threshold and ignored branch lengths below it. This eliminates a bias that could arise due to the addition of arbitrarily small branches among identical sequences during phylogenetic inference. We conducted a ML delimitation analysis in mPTP, allowing a unique coalescent rate for each delimited species. We estimated support for the ML delimitation using 10 MCMC runs, each 1×10^7 generations long. Convergence between the different MCMC runs was assessed using the average standard deviation of delimitation support values across all runs.

We compiled a six-locus dataset (CYTB, BRCA1, IRBP, OGT, SLC38, and Anon128) in which a single exemplar specimen was chosen to

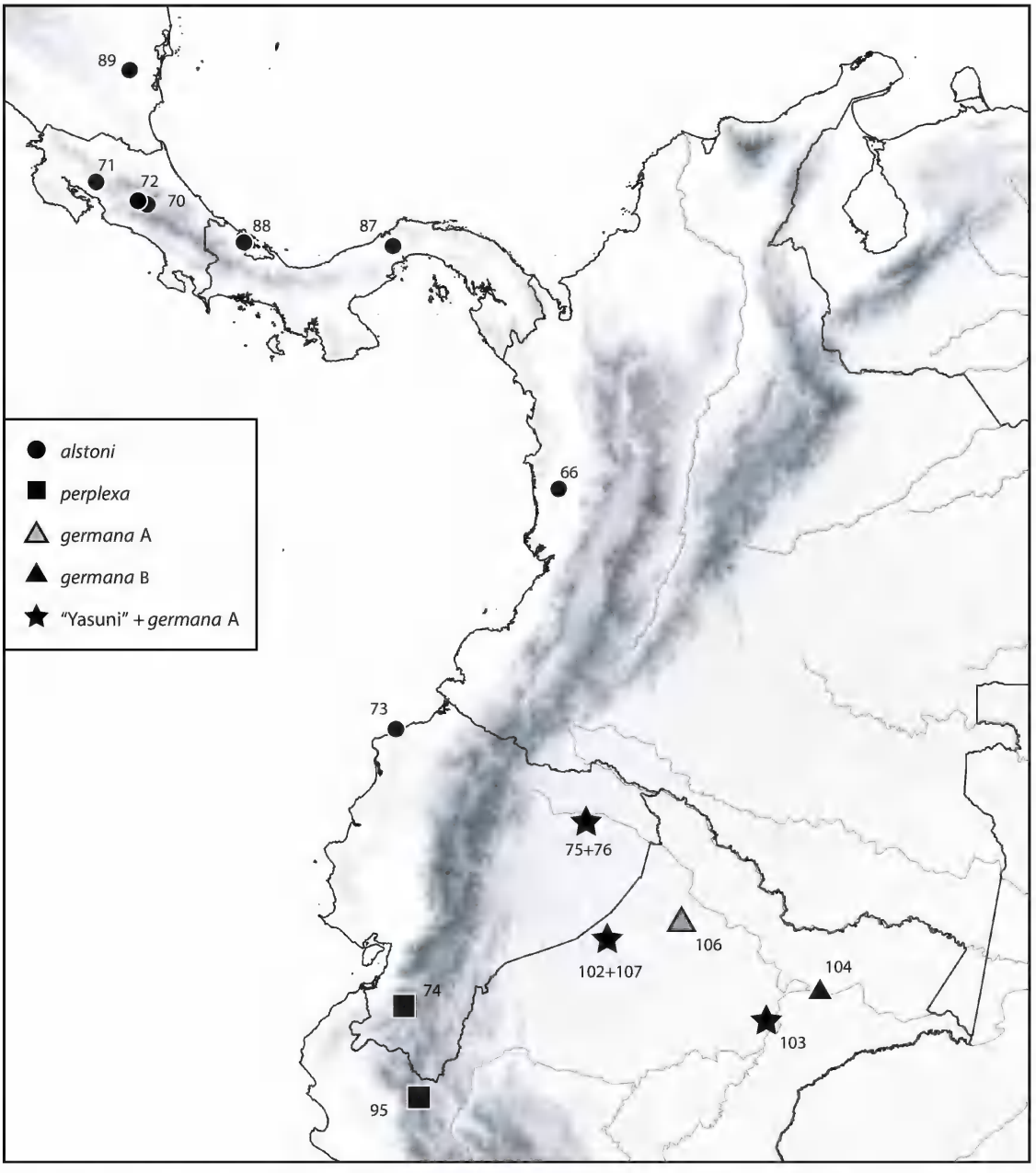


FIG. 1. Collection localities for sequenced specimens of *Marmosa* (*Micoureus*) corresponding to the putative species (haplogroups) *alstoni*, *perplexa*, *germana* A, *germana* B, and "Yasuni." Numbers are keyed to localities listed in appendix 1. Symbols for sympatry include records from localities separated by <10 km without intervening riverine or other known barriers to dispersal.

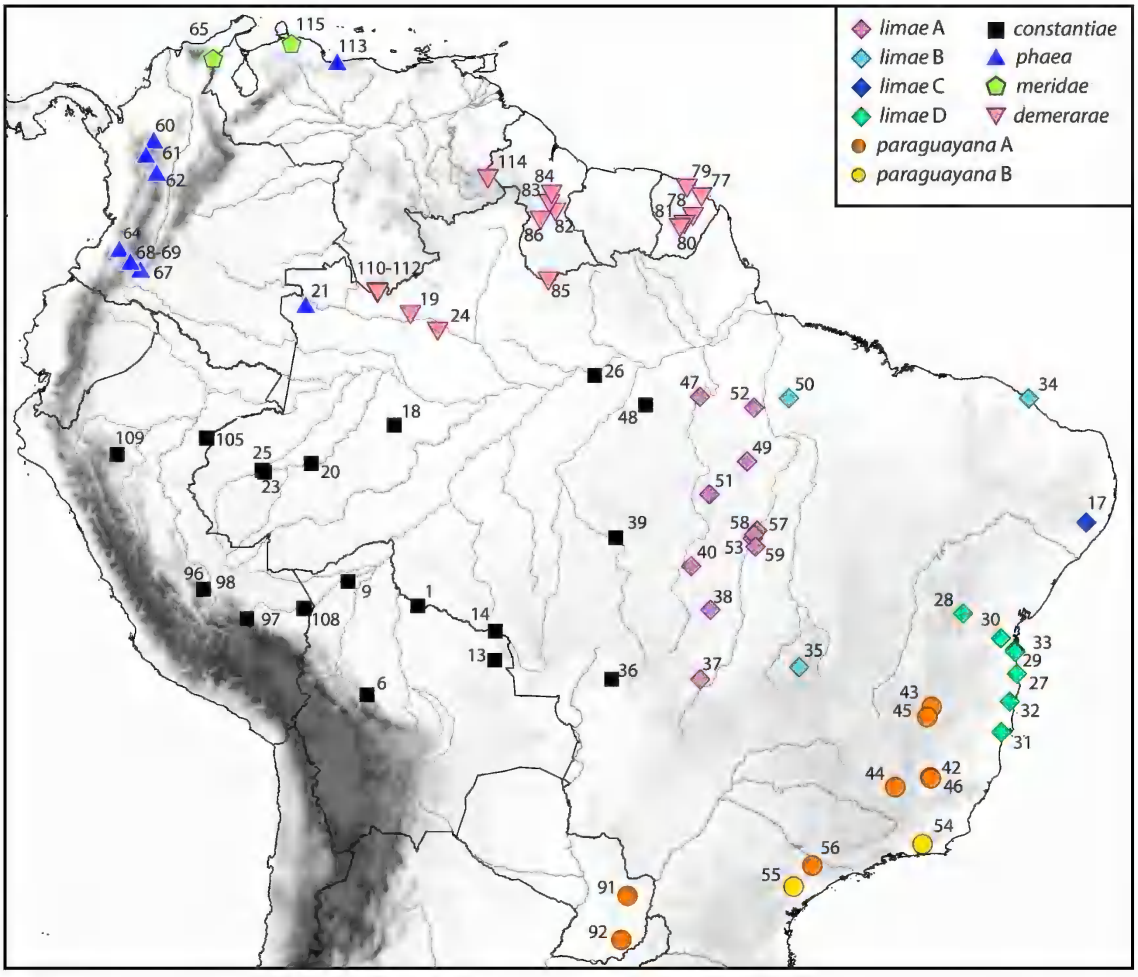


FIG. 2. Collection localities for sequenced specimens of *Marmosa* (*Micoureus*) corresponding to the putative species *constantiae*, *demerarae*, *limae* A–D, *meridae*, *paraguayana* A, *paraguayana* B, and *phaea*. Numbers are keyed to localities listed in appendix 1.

represent each mPTP-delimited putative species. A maximum-likelihood tree was estimated from these concatenated data using IQ-TREE and the procedures described above for the CYTB analysis. This dataset was divided into 12 subsets: one for each codon position in the protein-coding genes (CYTB, BRCA1, IRBP) and one each for the noncoding loci (OGT, SLC38, Anon128). Nodal support was calculated using 1000 ultrafast bootstrap replicates.

We inferred a Bayesian tree with MrBayes 3.2.6 (Ronquist et al., 2012). Prior to Bayesian inference, we tested nucleotide substitution models and partitioning schemes on the subset of models available in MrBayes using PartitionFinder2 (Lanfear et al., 2016). We allowed for the same data subsets as described for the multilocus IQ-TREE analysis. In MrBayes, we applied the best-fitting substitution models and partitioning scheme. We ran the analysis for 10^7 generations, initiating two independent MCMC runs, each with four chains. MCMC convergence was assessed in Tracer 1.7.1 (Rambaut et al., 2018). The posterior sample of trees was summarized in MrBayes after discarding 25% of the sample as burn-in.

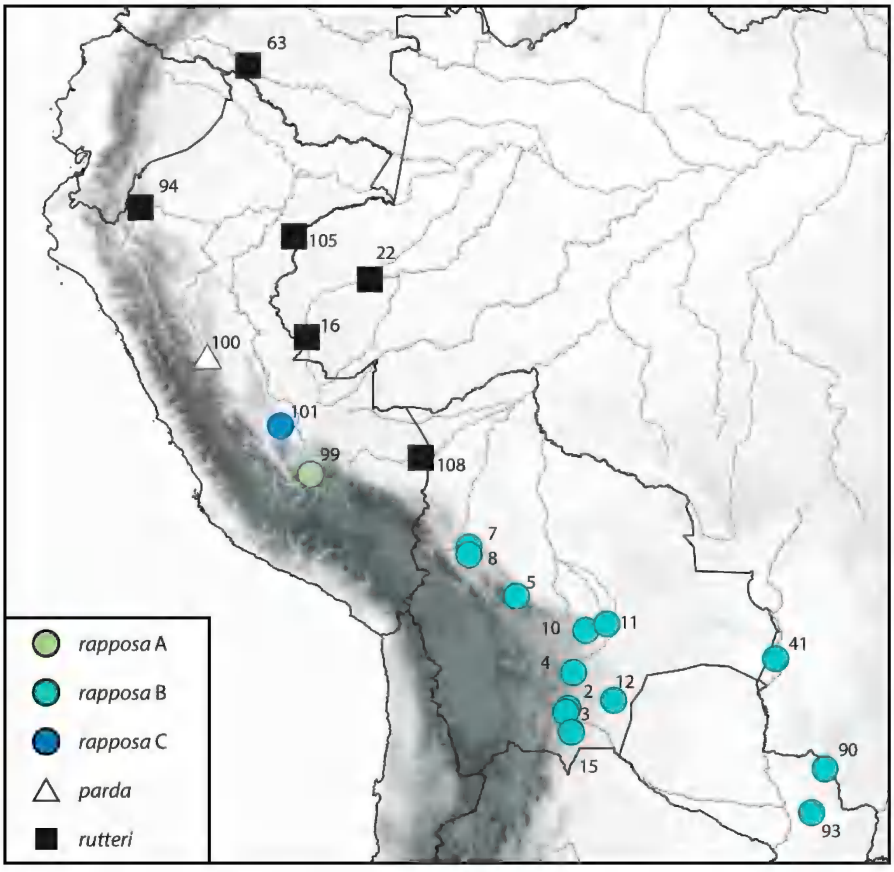


FIG. 3. Collection localities for sequenced specimens of *Marmosa* (*Micoureus*) corresponding to the putative species *parda*, *rapposa* A–C, and *rutteri*. Numbers are keyed to localities listed in appendix 1.

MEASUREMENTS: Except as noted otherwise, external measurements are those taken in the field by collectors using the standard American protocol (Hall, 1962). We transcribed total length (nose to fleshy tail tip, TL) and length of tail (basal flexure to fleshy tip, LT) from specimen labels or field notes, and we computed head-and-body length (HBL) by subtracting LT from TL. We also transcribed length of hind foot (heel to tip of longest claw, HF), length of ear (from notch, Ear), and weight from specimen labels or field notes, but we sometimes remeasured HF on fluid-preserved specimens to check the accuracy of values recorded by collectors, and we used our values whenever large discrepancies were found. All external measurements are reported to the nearest millimeter (mm), and all weights are reported to the nearest gram (g).

Craniodental measurements were taken with digital calipers and recorded to the nearest 0.01 mm, but values reported herein are rounded to the nearest 0.1 mm (the smallest decimal fraction of a millimeter that is consistently obtainable with repeated caliper measurements). The following dimensions were measured (fig. 4):

Condylobasal length (CBL): Measured from the occipital condyles to the anteriormost point of the premaxillae

Nasal breadth (NB): Measured across the triple-point sutures of the nasal, frontal, and maxillary bones on each side

Least interorbital breadth (LIB): Measured at the narrowest point across the frontals between the orbits

TABLE 3

Ingroup and Outgroup Sequences Used for Multigene Phylogenetic Analyses

	CYTB[a]	Nuclear loci[a]				
		Anon128	BRCA1	IRBP	OGT	SLC38
INGROUP:						
alstoni	MN978600	MN978682	MN978694	MN978706	MN978713	MN978725
constantiae	HM106375		FJ159304	AF257693	KM071234	KM071140
demerarae	MN978623	MN978683	MN978695	MN978707	MN978714	
germana A	MN978627	MN978684	MN978696	MN978708	MN978715	
germana B	MN978632	MN978685	MN978697		MN978716	
limae A	MN978634	MN978686	MN978698		MN978717	
limae B	EF587292					
limae C	JF281091					
limae D	MN978639	MN978687	MN978699		MN978718	
meridae	MN978642	MN978688	MN978700		MN978719	
paraguayana A	MN978643					
paraguayana B	HM106373	KU171148	FJ159305		KJ129917	KJ129974
parda	MN978644					
perplexa	MN978646	MN978689	MN978701	MN978709	MN978720	MN978726
phaea	MN978648	MN978690	MN978702		MN978721	
rapposa A	MN978658					
rapposa B	MN978669	MN978691	MN978703	MN978710	MN978722	MN978727
rapposa C	MN978675	MN978692	MN978704	MN978711	MN978723	MN978728
rutteri	MN992051	KU171149	FJ159306	AY233780	KM819064	MN978729
"Yasuni"	MN978679	MN978693	MN978705	MN978712	MN978724	
OUTGROUP:						
Thylamys pusillus	HM583416	KJ129877	FJ159319	AY957489	KJ129934	KJ129959

[a] Column entries are GenBank accession numbers.

Least postorbital breadth (LPB): Measured at the narrowest point across the frontals between the temporal fossae (behind the postorbital processes)

Zygomatic breadth (ZB): Measured at the widest point across both zygomatic arches

Palatal length (PL): Measured from the anteriormost point of the premaxillae to the postpalatine torus, including the postpalatine spine (if present)

Palatal breadth (PB): Measured across the labial margins of the fourth molar (M4) crowns, at or near the stylar A position

Maxillary toothrow length (MTR): Measured from the anterior margin of the canine (C1) to the posterior margin of the fourth molar (M4)

Length of molars (LM): Measured from the anteriormost labial margin of M1 to the posteriormost point on M4

Length of M1–M3 (M1–M3): Measured from the anteriormost labial margin of M1 to the posteriormost point on M3

Width of M3 (WM3): Measured from the labial margin of the crown at or near the stylar A position to the lingual apex of the protocone

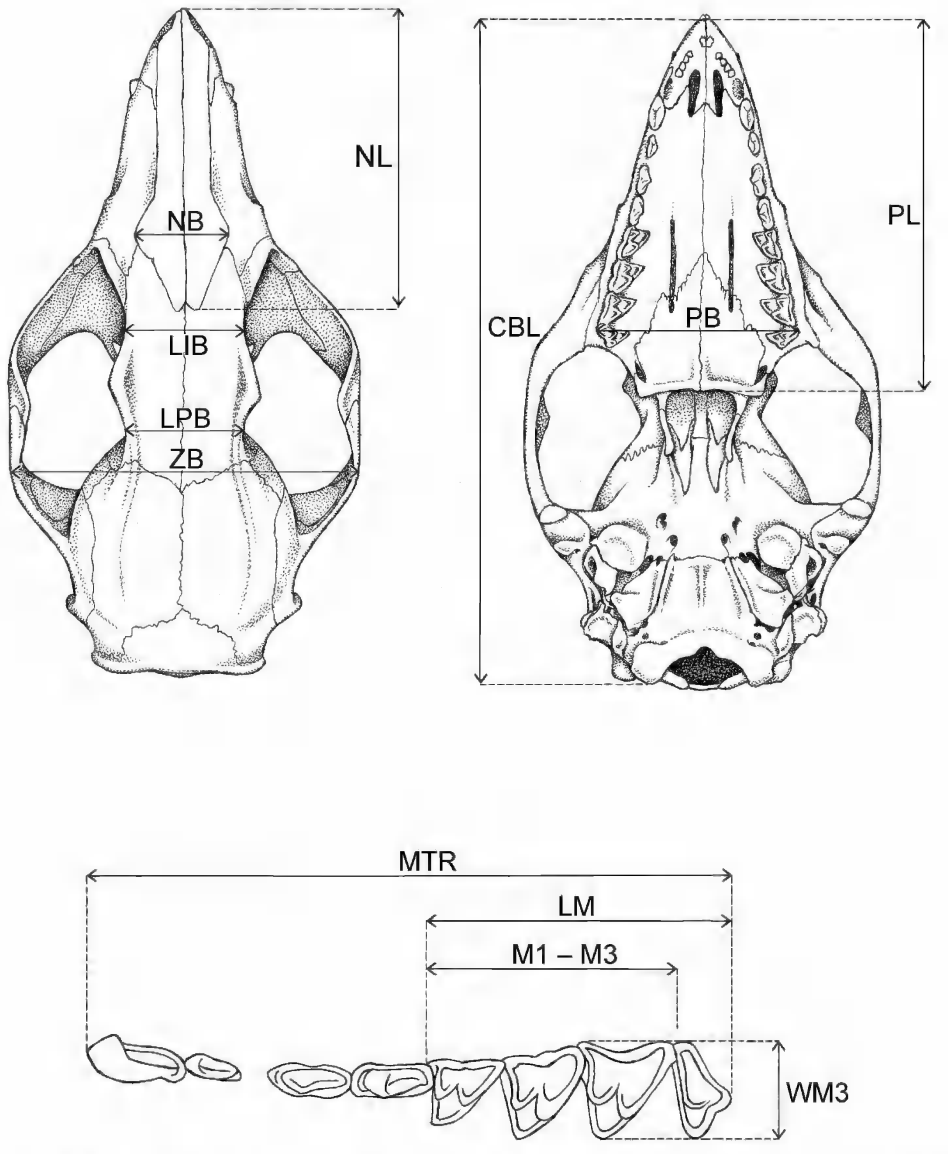


FIG. 4. Dorsal and ventral cranial views and occlusal view of the maxillary dentition of *Marmosa murina* (not a member of the subgenus *Micoureus*), showing the anatomical limits of craniodental measurements defined in the text.

AGE DETERMINATION: Except as noted below, all analyzed morphological character data were obtained from adult specimens as determined by dental criteria. The third upper and lower premolars (P3/p3) are the last teeth to erupt in *Marmosa*, and we used the maxillary locus to define age classes: a specimen was judged to be *juvenile* if the deciduous third premolar (dP3) was still in place; *subadult* if dP3 had been shed, but P3 was still incompletely erupted; and *adult* if the permanent upper dentition was complete. In effect, specimens that we judged to be adult by these criteria correspond to age classes 6–9 of Rossi et al. (2010). Although we acknowledge that our adult material

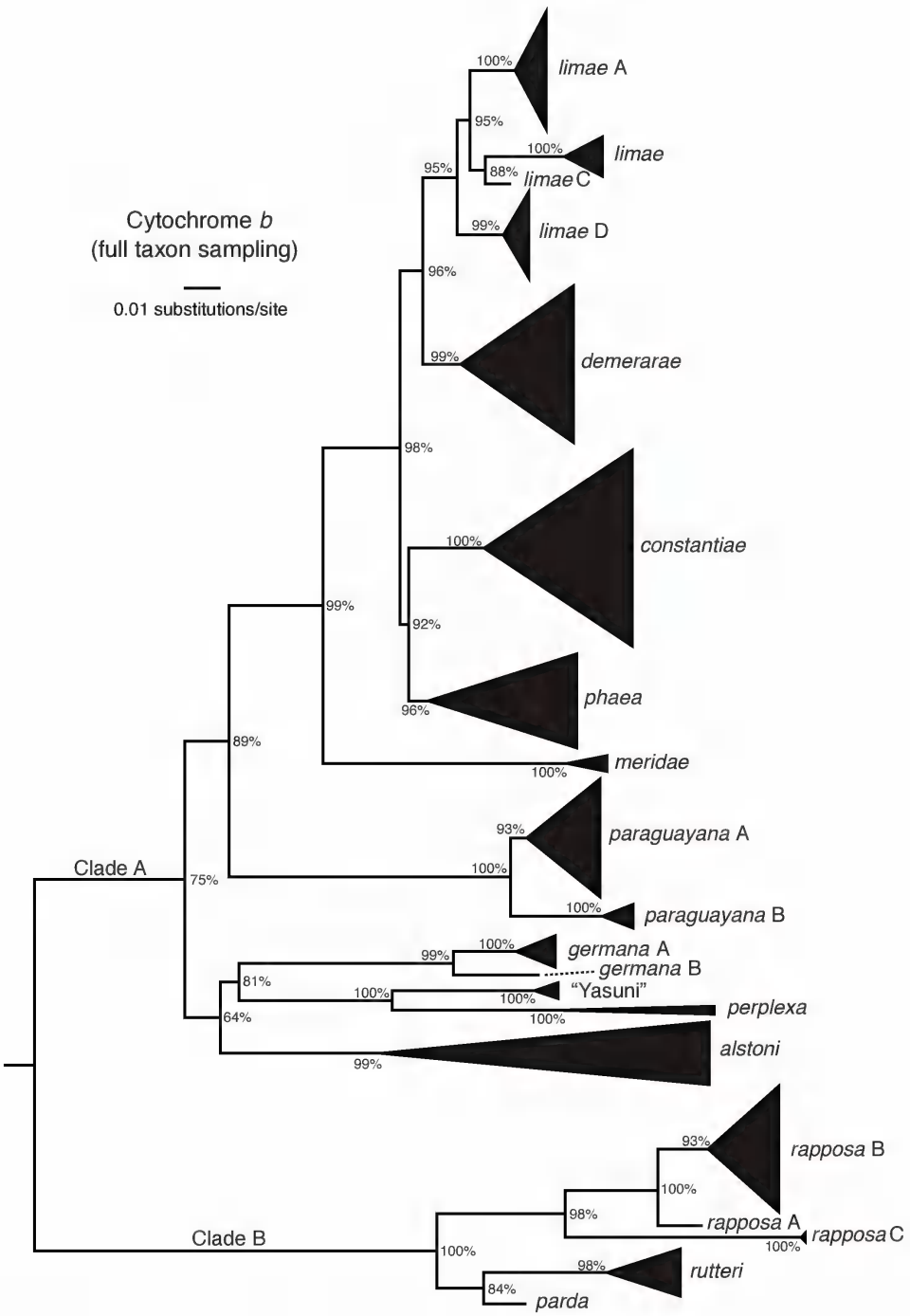


FIG. 5. Phylogenetic tree based on maximum-likelihood analysis of 167 cytochrome *b* sequences. Numbers at nodes denote ML bootstrap support. For haplogroups with more than one sequence, tips of the phylogeny have been collapsed into black triangles, the breadth of which is proportional to the number of sequences within each clade and the depth of which is proportional to genetic diversity. The outgroup is not shown.

exhibits substantial ontogenetic variation in many cranial dimensions (as evidenced by the tendency for specimens with more heavily worn teeth to have larger measurement values for most dimensions than specimens with unworn teeth), we were unable to consistently distinguish toothwear-defined age classes in our material.

MOLECULAR ANALYSES

Results

The mPTP analysis identified 21 putative species (95% credible interval = 17–25 species), of which 20 could be resolved as reciprocally monophyletic haplogroups (fig. 5). Across the 10 independent MCMC runs, the average support value for the ML delimitation of 21 species was 87.9%, and the standard deviation of support values was 0.00034. At the base of the tree is a robustly supported dichotomy that separates taxa belonging to two main clades, of which the larger (Clade A) includes 15 haplogroups and the smaller (Clade B) only five. Fourteen haplogroups in Clade A can be provisionally associated with named taxa, but one highly divergent haplogroup ("Yasuni") is unnamed. The putative species in Clade B can be confidently associated with named taxa based on revisionary research summarized in a subsequent section of this report.

Uncorrected average pairwise cytochrome *b* sequence comparisons among the putative species identified by mPTP range from 2% to 15%, but most values cluster in the range from 9% to 12% (table 4). Notably low values (2–4%) are mostly associated with comparisons among members of the monophyletic complex that includes *demerarae*, *limae* A, *limae* B, *limae* C, and *limae* D, but similarly low values were obtained for comparisons between *germana* A and *germana* B, between *paraguayana* A and *paraguayana* B, and between *rapposa* A and *rapposa* B. Average intraspecific distances (the bolded diagonal elements in table 4) are mostly small, but those for *alstoni* and *perplexa* are notably larger than the others.

All the putative species in figure 5, together with Clade B and several other internal nodes are robustly supported in this analysis of cytochrome *b* sequence data. Phylogenetic analyses based on the concatenated-gene dataset (fig. 6) provide strong support for most of the internal nodes that they have in common, including Clade A and Clade B. Additionally, there is robust support in the concatenated-gene data for the nested relationships (*meridae* (*phaea* (*constantiae* (*demerarae* + *limae*)))), for *paraguayana* A + *paraguayana* B, for *perplexa* + "Yasuni," for *germana* A + *germana* B, and for (*rapposa* C (*rapposa* A + *rapposa* B)). By contrast, one or both concatenated-gene analyses provide only weak support for the shared clades (*alstoni* (*germana* A + *germana* B)) and *parda* + *rutteri*. Topological differences between the maximum-likelihood and Bayesian results for these data concern relationships that are not strongly supported in either analysis.

Discussion

Single-locus species delimitation methods are useful for identifying operational taxonomic units that can subsequently be analyzed using other data. However, as repeatedly emphasized in the literature (e.g., Carstens et al., 2013; Sukumaran and Knowles, 2017), these methods provide an inadequate basis for taxonomic inference on their own merits, so the putative species recovered by mPTP in this study should not be interpreted as valid taxa without additional supporting evidence. Nevertheless, the number of putative species recovered by mPTP and the substantial pairwise distances among some of them suggest that the subgenus *Micoureus* is more diverse than currently recognized. Later in this report we formally revise the species in Clade B based on morphological comparisons, but revisions of the species in Clade A are still in progress, and only preliminary remarks about geographic distributions and the application of names can be offered here.

TABLE 4

Mean Uncorrected Pairwise Sequence Divergence at the Cytochrome *b* Locus within and among Putative Species of *Marmosa* (*Micoureus*)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1. *alstoni*	**0.05**																			
2. *constantiae*	0.10	**0.03**																		
3. *demerarae*	0.09	0.05	**0.02**																	
4. *germana* A	0.09	0.10	0.10	**0.01**																
5. *germana* B	0.09	0.09	0.09	0.04	—															
6. *limae* A	0.10	0.06	0.04	0.10	0.10	**0.01**														
7. *limae* B	0.10	0.05	0.04	0.10	0.10	0.04	**0.01**													
8. *limae* C	0.09	0.05	0.04	0.10	0.09	0.03	0.03	—												
9. *limae* D	0.09	0.05	0.04	0.10	0.09	0.03	0.04	0.02	**0.00**											
10. *meridae*	0.10	0.08	0.08	0.11	0.11	0.09	0.09	0.08	0.08	**0.01**										
11. *paragua.* A	0.10	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.09	0.09	**0.01**									
12. *paragua.* B	0.11	0.09	0.10	0.09	0.10	0.09	0.09	0.08	0.09	0.09	0.04	**0.01**								
13. *parda*	0.11	0.13	0.13	0.12	0.12	0.13	0.13	0.13	0.14	0.13	0.11	0.12	—							
14. *perplexa*	0.11	0.11	0.11	0.10	0.10	0.11	0.12	0.11	0.10	0.12	0.11	0.12	0.13	**0.05**						
15. *phaea*	0.10	0.06	0.05	0.10	0.10	0.05	0.05	0.05	0.05	0.08	0.09	0.10	0.14	0.11	**0.03**					
16. *rapposa* A	0.12	0.12	0.12	0.11	0.12	0.11	0.12	0.12	0.12	0.13	0.10	0.10	0.06	0.13	0.12	—				
17. *rapposa* B	0.13	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.14	0.11	0.12	0.06	0.15	0.14	0.03	**0.01**			
18. *rapposa* C	0.13	0.15	0.15	0.13	0.14	0.15	0.15	0.15	0.15	0.15	0.12	0.12	0.06	0.15	0.15	0.07	0.08	**0.00**		
19. *rutteri*	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.12	0.13	0.13	0.12	0.12	0.05	0.14	0.13	0.07	0.08	0.09	**0.02**	
20. "Yasuni"	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.10	0.09	0.10	0.09	0.10	0.13	0.08	0.10	0.12	0.13	0.14	0.13	**0.01**

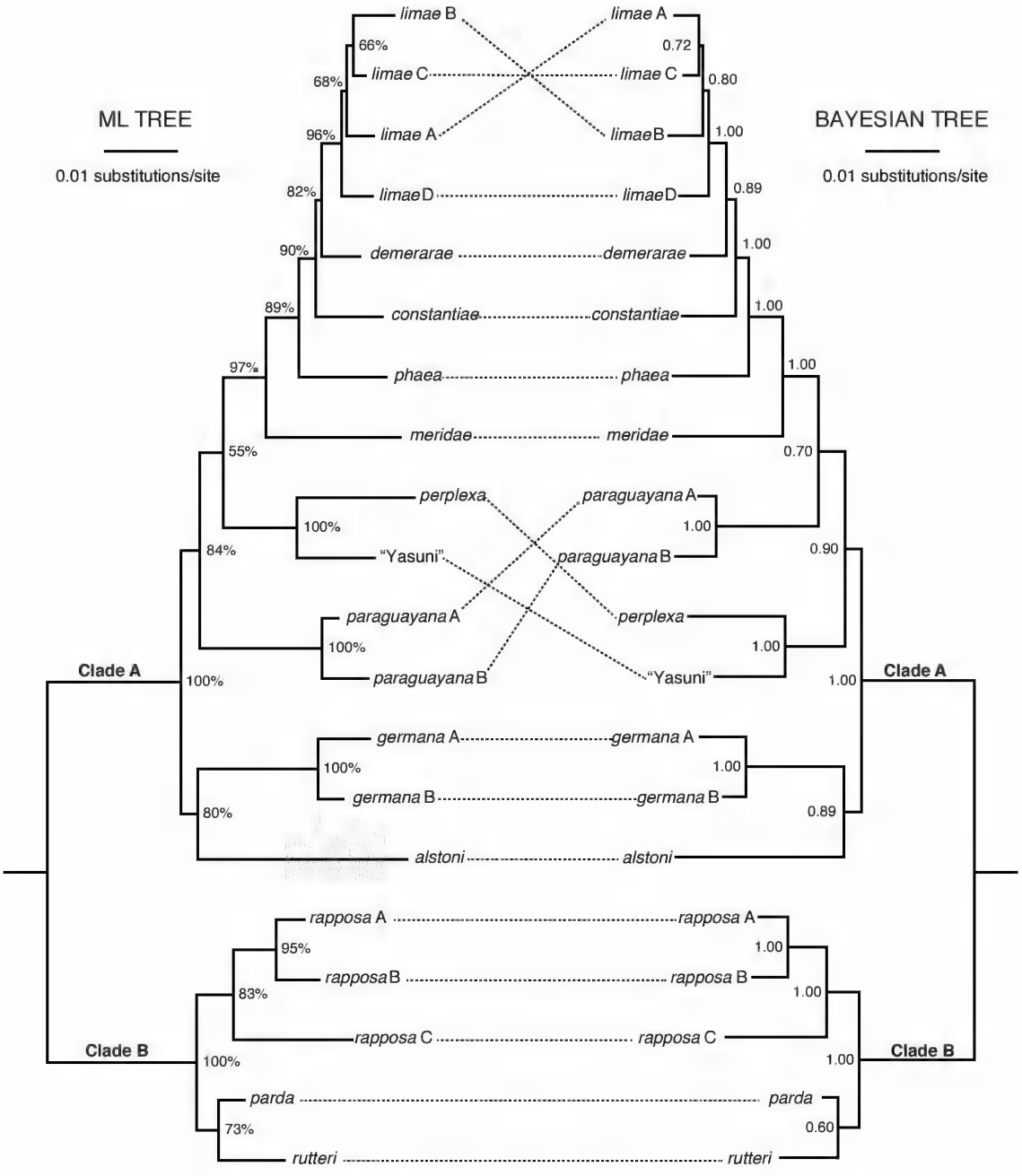


FIG. 6. Maximum-likelihood (left) and Bayesian (right) phylogenetic trees inferred from concatenated sequences of six genes (CYTB, BRCA1, IRBP, OGT, SLC38, and Anon128). Numbers at nodes denote ML bootstrap support or Bayesian posterior probabilities. Outgroups are not shown. Dotted lines connect the same taxon across the two trees to highlight differences.

Working our way downward from the top of the cartooned cytochrome *b* tree (fig. 5), the oldest name for *demerarae*-like specimens from southeastern Amazonia is *limae*, the application of which is supported by a 498 bp fragment of cytochrome *b* that we obtained from the holotype. The latter was recovered as a member of *limae* B, which occurs east of the Tocantins in the Brazilian states of Ceará, Goiás, and southeastern Pará (fig. 2). Based solely on geography, it seems probable that *pfrimeri* (with type locality in Goiás; table 1) is a synonym of *limae*, but we have not seen the lectotype. No names are apparently available for the putative species we call *limae* A (which occurs west of the Tocantins and east of the Xingu in the states of Mato Grosso, Pará, and Tocantins), *limae* C (from Alagoas), and *limae* D (from Bahia). However, pairwise distances among these four haplogroups are all small-to-modest (2%–4%), and we are not convinced that they are usefully recognized as distinct taxa. We have not made a close morphological study of this complex, which might not, in fact, be phenotypically distinguishable from *demerarae*.

The haplogroup we call *demerarae* includes all the sequences obtained from specimens collected north of the lower Amazon and east of the Rio Negro–Orinoco (the Guiana Region of zoogeographers; Tate, 1939). The type locality of *demerarae* is in Guyana, from which we have several representative sequences, and this haplogroup also includes sequences from specimens collected reasonably near the type localities of *arenticola*, and *esmeraldae*, which we provisionally regard as synonyms following Gardner and Creighton (2008). However, not all the specimens with sequences assigned to this putative species share the phenotypic traits traditionally associated with *demerarae*, an issue that will eventually need to be addressed in a revisionary context.

The application of the name *constantiae* in our results is supported by a topotypical sequence (from OMNH 37209; table 2), as well as by the morphological similarity of sequenced specimens from Mato Grosso and easternmost Bolivia with Thomas's (1904a) description and type material. Our distributional concept of *constantiae* is similar to Silva et al.'s (2019), including sequences from specimens collected south of the Amazon from the lower slopes of the Andes to the right bank of the Tapajós. However, there is geographic variation in external morphology (Voss et al., 2019), as well as phylogeographic structure within *constantiae*, both of which merit future revisionary attention. Based on our examination of type material, the nominal taxa *mapiriensis* (from the Andean foothills of Bolivia) and *domina* (from the left bank of the Tapajós) are probably synonyms of *constantiae*.

The sequences we assign to *phaea* (next in vertical sequence after *constantiae* in fig. 5) are from a widely scattered array of localities that extend from the Colombian Andes to the coastal mountains of northern Venezuela and the Amazonian lowlands of northwestern Brazil. Although we have not made a close study of all the voucher material for sequences assigned to this clade, the specimens we sequenced from the Colombian departments of Cauca and Huila resemble the type series of *phaea* (from Nariño), whereas other specimens (e.g., those from lowland Antioquia) exhibit obvious morphological differences. There is, additionally, strongly developed phylogeographic structure in this problematic haplogroup, which clearly warrants future study.

The highly divergent haplogroup that we tentatively identify as *meridae* includes sequences from specimens collected at two localities, one in northern Colombia and the other in northwestern Venezuela. This material is phenotypically similar to the holotype and topotypical material of *meridae*, but the type locality is not particularly close to where the vouchers were collected (Mérida is about 270 km SE of locality 65 and about 380 km SW of locality 115; fig. 2). Topotypical sequence data should help determine whether *meridae* is the name that properly applies to this clade.

Sister to the complex of mostly Amazonian and northern-Andean haplogroups described above is a clade consisting of two putative species

from the Atlantic Forest biome (the Mata Atlântica of Brazilian authors), both of which we associate with the name *paraguayana*. Whereas *paraguayana* A includes sequences from eastern Paraguay (the type locality of *paraguayana*) the other haplogroup, *paraguayana* B, includes a sequence from the Brazilian state of Rio de Janeiro—the type locality of *travassosi*. Without having seen the type of *travassosi* we hesitate to use the name even in this informal context, preferring to maintain the prevailing usage of *paraguayana* as the currently accepted senior synonym. However, the two haplogroups are about 4% divergent, on average, and they occur at adjacent localities in the state of São Paulo (appendix 1). The few specimens we examined (N = 15; from Paraguay, Minas Gerais, Rio de Janeiro, and São Paulo) exhibit no conspicuous character variation inter se, but the woolly mouse opossums of the Atlantic Forest would seem to merit taxonomic attention based on these results.

Two haplogroups that we associate with the name *germana* were obtained from specimens collected north of the Amazon in eastern Ecuador and northeastern Peru (fig. 1). Although *germana* is currently treated as a subspecies of *regina*,[2] this is an unambiguously distinct lineage, the relationships of which are, apparently, either with *perplexa* + "Yasuni" (fig. 5) or with *alstoni* (fig. 6). However, our morphological material of *germana* does not closely resemble voucher specimens of any of the putative species with which it is associated phylogenetically. Whereas Gardner and Creighton (2008) treated *parda* and *rutteri* as junior synonyms of *germana*, we recognize *parda* and *rutteri* as valid species of the Rapposa Group (see below).

The sister-group relationship of *perplexa* and "Yasuni" is strongly supported in all our phylogenetic results. Although the former name has long been treated as a synonym of *phaea*, the cytochrome *b* sequences we refer to *perplexa* (from western Ecuador and northern Peru; see above) and *phaea* (from Colombia, northwestern Brazil, and northern Venezuela) are highly divergent (about 11%), and none of our analyses recovered them as sister lineages. Specimens of "Yasuni" (an Amazonian lineage from eastern Ecuador and northeastern Peru) are morphologically distinctive and do not closely resemble *perplexa* or any other nominal taxon. Our current working hypothesis is that they represent an undescribed species.

The haplogroup that we identify as *alstoni* includes sequences from specimens collected in Central America and in the trans-Andean lowlands of western Colombia and northwestern Ecuador. This haplogroup is strongly structured phylogeographically, and the associated voucher material is morphologically heterogeneous, including some of the largest and some of the smallest specimens in the subgenus. The next installment of our revisionary series will treat this haplogroup in substantive detail, but for now we follow the currently accepted taxonomy (Gardner, 2005), which treats *nicaraguae* as a junior synonym of *alstoni*.

COMPARATIVE MORPHOLOGY

The mitochondrial lineages of *Marmosa* (*Micoureus*) recognized as valid species in this report and those that follow can be phenotypically distinguished from one another by qualitative morphological characters and measurement data. Here we describe character variation among examined skins and skulls using anatomical terminology explained or referenced by Voss and Jansa (2003, 2009), with exceptions as noted below.

Size and External Morphology

Species of the subgenus *Micoureus* are externally rather similar, but they are consistently distinguishable from other congeners by their dull-colored (usually brownish-gray, never distinctly reddish) dorsal fur, large manual claws (typically extending just beyond the fleshy digital

[2] As explained elsewhere (Voss et al., 2019: 31), we follow Tate (1933: 83) in restricting the name *regina* to the holotype, which is strikingly unlike other nominal taxa of the subgenus *Micoureus*.

pad on each finger), possession of lateral and medial carpal tubercles in large adult males, and tails with rhomboidal scales in distinctly spiral series (Voss et al., 2014). However, some sympatric species of *Micoureus* are so alike externally that it can be difficult to tell them apart, with the result that field identifications are often challenging. Careful attention to age criteria, accurate external measurements, subtle differences in pelage length and pigmentation, and tail markings, however, can be taxonomically informative.

SIZE: Members of the subgenus *Micoureus* include the largest known species of *Marmosa*, but interspecific size differences within *Micoureus* are substantial. The smallest species is an unnamed Panamanian form with an average adult head-and-body length of 139 mm (observed range 121–150 mm; $N = 7$) and an average adult weight of just 58 g (observed range 40–68 g; $N = 5$). By contrast, *Marmosa rutteri*, one of the larger species, has an average adult head-and-body length of 179 mm (observed range 152–251 mm; $N = 32$) and an average adult weight of 122 g (observed range 63–180 g; $N = 28$). However, as can be seen from the observed ranges, there is substantial intraspecific variation in these dimensions, including sexual size dimorphism as well as ontogenetic variability among the specimens classed as "adults" (see Materials and Methods). The latter typically include smaller (presumably younger) individuals with almost-unworn dentitions and larger (presumably older) individuals with heavily worn teeth. Because sexual size dimorphism and ontogenetic variability are minimal for molar dimensions—which (unlike head-and-body length or weight) can be determined with high accuracy from museum specimens—we often use upper-molar toothrow length (LM) as a surrogate for size in species comparisons. For the unnamed Panamanian species mentioned above, LM averages 7.6 mm (observed range 7.3–8.0, $N = 8$); for *M. rutteri*, LM averages 9.0 mm (observed range 8.3–9.8 mm, $N = 56$).

DORSAL PELAGE: The dorsal fur of *Micoureus* is often described as "woolly" (e.g., by Gardner and Creighton, 2008) because the individual hairs of some species are strongly kinked. This trait is most pronounced in longer-furred taxa (e.g., *M. alstoni*, *M. paraguayana*), whose pelage has a distinctively fluffy texture, but it is less pronounced in shorter-furred species (e.g., *M. rutteri*). Fur length is positively correlated with altitude in species with wide elevational distributions (e.g., *M. rapposa*), although some lowland populations of *M. demerarae* are also long furred. Dorsal fur color in *Micoureus* is almost always some dull shade of brownish gray, but *M. paraguayana* has distinctively clear-grayish dorsal fur, at least in the few fresh skins we examined.

VENTRAL PELAGE: The ventral fur is taxonomically variable in the subgenus *Micoureus*, as it is in many other small opossums. Following Tate (1933), we use the prefix "self-" in combination with descriptors of ventral pelage color (e.g., self-yellow) to describe fur comprised of hairs that have the same coloration from base to tip; by contrast, fur comprised of hairs that are basally gray is described as "gray based" (gray-based yellow, for example). Whereas almost the entire ventral pelage can be self-colored in some species (e.g., *M. rapposa*), others (e.g., *M. demerarae*) have extensively gray-based ventral fur (fig. 7). Commonly, however, the ventral pelage includes both types of fur, sometimes with a self-colored midventral streak that extends from chin to groin and lateral zones of gray-based fur between the fore- and hind legs.

GULAR GLAND: Adult male specimens of many opossums, including some species of *Marmosa*, have a naked patch of glandular skin on the midline of the throat or upper chest. Although the absence of such a gular gland was listed as a diagnostic trait of the subgenus *Micoureus* by Voss et al. (2014), a distinct gular gland is present on the holotype of *Marmosa regina* (BMNH 98.5.15.4), an old adult male (Thomas, 1898). Whether this is an individual peculiarity or a consistent trait of the species—currently known from a single specimen—is unknown.

TAIL: The tail is always substantially longer than the combined length of the head and body in

FIG. 7. Taxonomic variation in ventral pelage color as exemplified by *Marmosa rapposa* (on the left, with self-yellow ventral fur) and *M. demerarae* (right, with gray-based yellow ventral fur). From left to right: AMNH 210398, 210399, 210400, 266427, 267370, 267818).

the subgenus *Micoureus*, with computed sample means of the ratio LT/HBL × 100 ranging from about 130% to almost 150%. Unfortunately, artifactual variation in external dimensions measured in the field by different collectors is sufficiently high that relative tail length is generally unsuitable for diagnosis or identification. Instead, other caudal features are more consistently useful.

Soft body pelage ("fur" in the ordinary sense of the word) extends onto the base of the tail to a taxonomically variable extent, and this character is sometimes useful for distinguishing sympatric species (Patton et al., 2000). In many species (e.g., *M. parda*, *M. perplexa*, *M. rapposa*, *M. rutteri*) body fur extends for only a short distance (≤ 20 mm) along the base of the tail, and the caudal fur is short, resembling the condition seen in other subgenera of *Marmosa*. By contrast, in several other species (e.g., *M. alstoni*, *M. demerarae*, *M. meridae*, *M. paraguayana*), body fur extends for 25 mm or more (to 55 mm in some specimens) along the base of the tail, and in these same taxa the caudal fur also tends to be long (with hairs >10 mm), resulting in a conspicuously fluffy tail base (fig. 8).

The pigmentation of the unfurred (scaly) part of the tail is also taxonomically variable in *Micoureus*. In most species—including *Marmosa germana*, *M. parda*, *M. perplexa*, and *M. rutteri*—the scaly part of the tail is entirely dark (grayish or brownish) from base to tip, resembling the widespread, uniform caudal coloration seen in other subgenera. In others, however, the base of the tail is dark but the distal part is

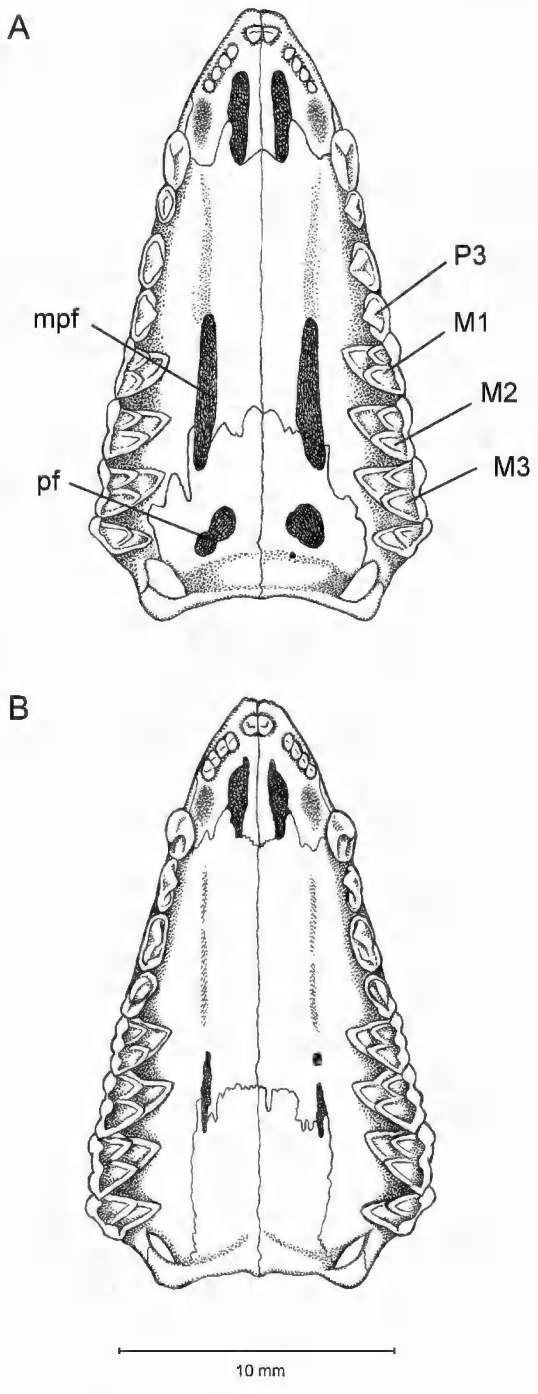
FIG. 8. Taxonomic variation in tail pelage and coloration as exemplified by *Marmosa parda* (left, with short-furred tail base and all-dark integument) and *M. alstoni* (right, with long-furred tail base and particolored integument. From left to right: FMNH 24137, 24138, 24139; AMNH 139280, LSUMZ 12636, AMNH 140379.

unpigmented (whitish or pinkish in life); this, the "particolored" phenotype (Voss and Jansa, 2009: 25), is the usual condition in *M. alstoni*, *M. meridae*, *M. nicaraguae*, *M. rapposa*, *M. paraguayana*, and in some forms of the *M. demerarae* complex (fig. 8). A few species are polymorphic for pale caudal markings, but one condition or the other seems to predominate in most taxa.

Craniodental Morphology

Adult skulls of members of the subgenus *Micoureus*, like those of species in other subgenera of *Marmosa*, have short, wide rostrums; large orbits; well-developed postorbital processes; widely flaring zygomatic arches; and small bullae. Indeed, species of *Micoureus* seem to be exceptionally conservative in craniodental morphology, with the result that skulls of even quite distantly related taxa are hard to tell apart. Only a few nonmetrical craniodental characters seem to be useful for the purposes of this revision, including details of palatal fenestration, the length of postprotocristae on the upper molars, and the occurrence of postcingulids on the lower molars.

Maxillopalatine fenestrae: Perforations in the didelphid hard palate include foramina and fenestrae (Voss and Jansa, 2009: 36–38). Spe-



cies of the subgenus *Micoureus* can have as many as four pairs of palatal perforations, including (from front to back) the incisive foramina, maxillopalatine fenestrae, palatine fenestrae, and posterolateral palatal foramina. All species have maxillopalatine fenestrae—nonvascular openings in the suture between the maxillary and palatine bones—but these can vary substantially in size. Maxillopalatine fenestrae are largest in species such as *Marmosa rapposa*, where they are wide and usually extend from a point opposite P3 to a point opposite M3 (fig. 9A), and they are smallest in species such as *M. germana*, where they are narrow and usually extend only from M1 to M2 (fig. 9B). However, many species have intermediate morphologies, and in all examined species there is appreciable variation in fenestral width and length.

Palatine fenestrae: Palatine fenestrae are openings contained entirely by the palatine bones, posterior to the maxillopalatine openings. In a few species, palatine fenestrae are normally present, but in others they are usually absent. As a result, although unilateral polymorphisms are not uncommon, this character is often useful for taxon diagnosis (e.g., Silva et al., 2019; Voss et al., 2019). For example, whereas palatine fenestrae are bilaterally present in 94% of examined specimens of *Marmosa rapposa* (fig. 9A), they are bilaterally absent in 100% of examined specimens of *M. germana* (fig. 9B).

Postprotocristae: Of the two enamel crests that diverge from the apex of the protocone on didelphid upper molars (Voss and Jansa, 2009: fig. 20), the preprotocrista passes anterolabially around the base of the paracone to join with the anterolabial cingulum, forming a continuous shelf along the anterior margin of the crown in all examined species of *Marmosa*. By contrast, the postprotocrista varies in length among species of the subgenus *Micoureus*. In species with a

FIG. 9. Ventral views of palates of *Marmosa rapposa* (**A**, MSB 104347) and *M. germana* (**B**, TTU 101236). Both species have maxillopalatine fenestrae (**mpf**), but these openings are much larger in *M. rapposa* than in *M. germana*, and only the former species has palatine fenestrae (**pf**). Dental loci (**P3**, **M1**, **M2**, **M3**) are convenient landmarks for describing fenestral size.

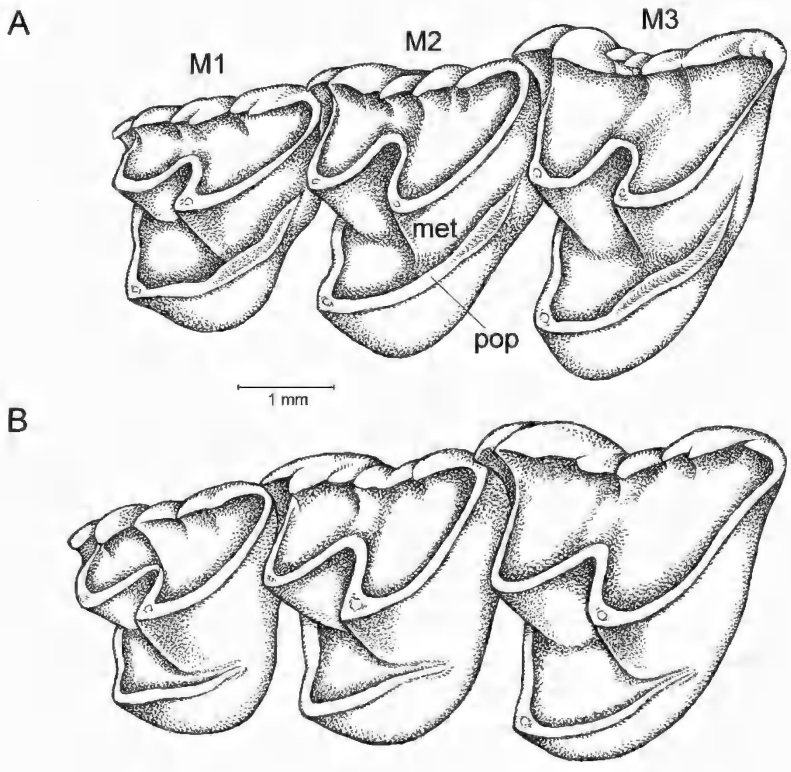


FIG. 10. Posterolingual views of left M1–M3 of *Marmosa rapposa* (**A**, AMNH 264923) and *M. constantiae* (**B**, MUSM 11062). In *M. rapposa*, the postprotocrista (**pop**) is long, extending labially beyond the base of the metacone (**met**) as a cingulum along the posterior surface of the tooth. By contrast, *M. constantiae* has a short postprotocrista that does not extend labially beyond the base of the metacone.

"long" postprotocrista (e.g., *M. rapposa*; fig. 10A), this crest extends labially far beyond the base of the metacone, forming a narrow cingulum along the posterior surface of the tooth (the "posterior lingual cingulum" of Silva et al., 2019). By contrast, in species with a "short" postprotocrista (e.g., *M. constantiae*; fig. 10B), this crest terminates at or near the base of the metacone, and the posterior surface of the crown labial to the metacone is smooth and essentially featureless. Although generally reliable for diagnostic purposes, the extent of the postprotocristae can sometimes be hard to assess in specimens with heavily worn teeth.

Posterior cingulids: The posterior cingulid—a well-known feature of tribosphenic dentitions that is also known as the postcingulid—is an enameled shelf that occurs along the posterobasal margin of the hypoconid on one or more lower molars in some species of the Rapposa Group.[3] This feature is best developed on unworn m1–m3 of *Marmosa rapposa* (fig. 11A), but it often persists even on the worn dentitions of old adults of this species. Although posterior cingulids are less well developed in other members of the Rapposa Group, a small posterior cingulid is usually present on m2 and sometimes also on m1 and/or m3 of *M. parda* and *M. rutteri* (see below). Other congeners (e.g., *M. constantiae*; fig. 11B) entirely lack this structure. Development of a posterior cingulid is correlated with the development of a

[3] Until quite recently (Voss et al., 2018), this structure was not known to occur in any didelphid, so it was omitted from Voss and Jansa's (2009: fig. 20) diagram of molar morphology. Outside the Rapposa Group of *Marmosa*, posterior cingulids are only known to occur in the recently described didelphine species *Philander pebas* (see Voss et al., 2018: fig. 20A).

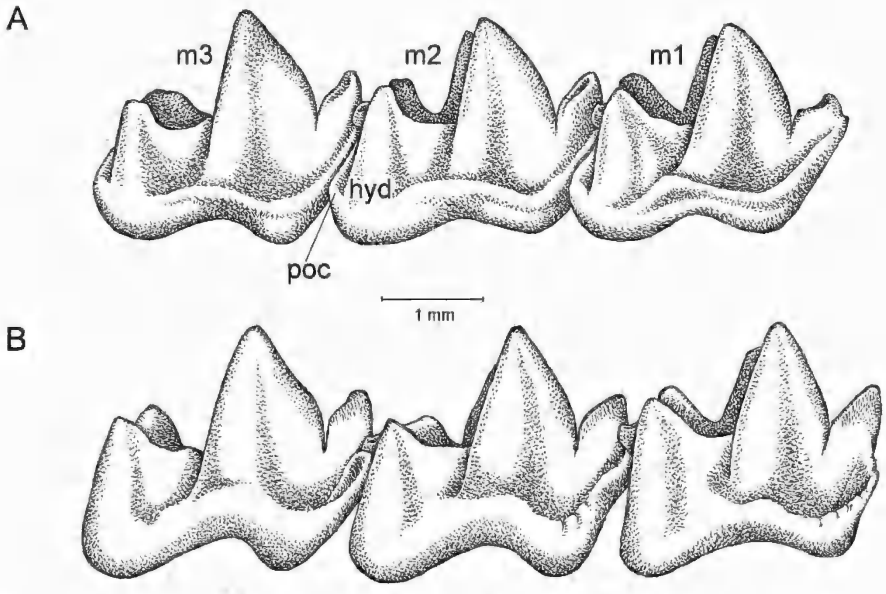


FIG. 11. Labial views of right m1–m3 of *Marmosa rapposa* (**A**, AMNH 264923) and *M. constantiae* (**B**, MUSM 11062). A small but distinct posterior cingulid (**poc**) is present at the base of the hypoconid (**hyd**) of each tooth in *M. rapposa*, whereas posterior cingulids are completely absent in *M. constantiae*.

labial cingulid (a shelf at the base of the hypoflexid; Silva et al., 2019: fig. 12), but in our experience the posterior cingulid provides a less subjective basis for scoring specimens.

TAXONOMIC ACCOUNTS

The following accounts summarize our conclusions about species limits in Clade B (hereinafter, the Rapposa Group) based on the molecular analyses described above and supporting morphological evidence. Our synonymies include only original descriptions, selected examples of usage represented in major works (e.g., Cabrera, 1958; Gardner, 2008), first instances of new name combinations, and incorrect subsequent spellings (if any). Except as noted otherwise, the species treated in this report conform to the morphological description of *Marmosa* provided by Voss and Jansa (2009: 101–104) and to the diagnosis of *Micoureus* in Voss et al. (2014). Therefore, only characters that vary within the subgenus are mentioned in the following accounts. Lists of specimens examined include only those personally seen by us. Locality information for examined specimens is abbreviated in the following accounts, but geographic coordinates and other details are provided in appendix 3.

The Rapposa Group

We recognize three species in the Rapposa Group ("Clade B" in figs. 5, 6), members of which are distinguished from other species of *Micoureus* by the absence of a fluffy-furred tail base, by their long postprotocristae, by the presence of posterior cingulids (postcingulids), and by their highly divergent cytochrome *b* sequences. Insofar as known, all members of the Rapposa Group are Andean or cis-Andean; none is trans-Andean, nor is any known to occur in the Atlantic Forest. Collectively, they occur along the eastern slopes of the Andes (below about 2500 m) from central Peru to northern Argentina; in the Amazonian lowlands of Colombia, Ecuador, Peru, and western Brazil; and in the Cerrado (or Cerrado-like) landscapes of eastern Bolivia, central Brazil, and Paraguay.

Marmosa (*Micoureus*) *rapposa*
Thomas, 1899

Marmosa rapposa Thomas, 1899b: 42 (original description).

Marmosa budini Thomas, 1920a: 195 (original description).

Marmosa constantiae constantiae: Tate, 1933: 75 (part, based on misidentified material), not *constantiae* Thomas, 1904a.

Marmosa constantiae budini: Tate, 1933: 76 (new name combination).

Micoureus constantiae: Gardner, 1993 (part; *budini* treated as synonym), not *constantiae* Thomas, 1904.

Micoureus regina: Gardner, 1993: 20 (part; *rapposa* treated as synonym), not *regina* Thomas, 1898.

Micoureus constantiae constantiae: Anderson, 1997: 156 (part; based on misidentified material), not *constantiae* Thomas, 1904a.

Micoureus constantiae budini: Anderson, 1997: 156 (new name combination).

Micoureus regina rapposo: Gardner and Creighton, 2008: 81 (new name combination with inappropriate gender change).[4]

Marmosa (*Micoureus*) *constantiae*: Voss and Jansa, 2009: 101 (part; *budini* treated as synonym), not *constantiae* Thomas, 1904a.

Marmosa (*Micoureus*) *regina*: Voss and Jansa, 2009: 101 (part; *rapposa* treated as synonym), not *regina* Thomas, 1898.

Marmosa (*Micoureus*) *constantiae*: de la Sancha et al., 2012 (misidentified material), not *constantiae* Thomas, 1904a.

Marmosa (*Micoureus*) *budini*: Silva et al., 2019: 254 (new name combination).

TYPE MATERIAL AND TYPE LOCALITY: The holotype (by original designation, BMNH 98.11.6.13) consists of the skin and skull of a large adult female collected by Otto Garlepp in December 1897 on the "Vilcanota River just north of Cuzco" (Thomas, 1899b: 43) at 1500 m elevation in the Peruvian department of Cusco. As noted by Jenkins and Knutson (1983), the catalog number of this specimen was incorrectly reported by Thomas (as 98.11.1.13). Four juvenile paratypes (BMNH 98.11.6.14–98.11.6.17, also collected by Garlepp at the same locality in December 1897) are assumed to be offspring of the holotype (Thomas, 1899b; Tate, 1933).

According to Ceballos-Bendezú (1981), the type material of *Marmosa rapposa* was collected at Huadquiña in the district of Santa Teresa, province of La Convención (district and province are sequentially larger administrative units of Peruvian departments). Stephen and Traylor's (1983) coordinates for Huadquiña (appendix 3: locality 52) place it ca. 85 km NW of Cuzco. According to Stephens and Traylor (1983) "Vilcanota" is a local synonym for the upper Urubamba.

DISTRIBUTION AND SYMPATRY: Based on specimens that we examined and others examined by Silva et al. (2019), *Marmosa rapposa* occurs along the eastern slopes of the Andes (below about 2500 m) and in adjacent foothills from about 13° S in southeastern Peru (Junín and Cuzco) to about 26° S in northwestern Argentina (Tucumán). Additionally, this species is widely distributed in the lowlands of eastern Bolivia, and we have also seen specimens from Brazil and Paraguay (fig. 12).

Marmosa rapposa occurs sympatrically with *M. constantiae* in eastern Bolivia (see below) and perhaps also in southeastern Peru, eastern Bolivia, and southwestern Brazil. Additionally, the geographic range of *M. rapposa* approaches that of *M. paraguayana* in eastern Paraguay (de la Sancha et al., 2012: fig. 2).[5]

DESCRIPTION: The dorsal pelage of *Marmosa rapposa* is uniformly drab, ranging from a dull yellowish-gray—somewhat similar to Ridgway's (1912) Grayish Olive—to a somewhat warmer

[4] "Raposa" is the vernacular term for opossum in Peruvian Spanish, so the epithet is to be understood as a noun standing in apposition to the generic name. Although incorrectly spelled according to Spanish orthography, *rapposa* is the correct original spelling in the sense of the Code (ICZN, 1999: article 32).

[5] But note that *Marmosa rapposa* is identified as *M. constantiae* by de la Sancha et al. (2012).

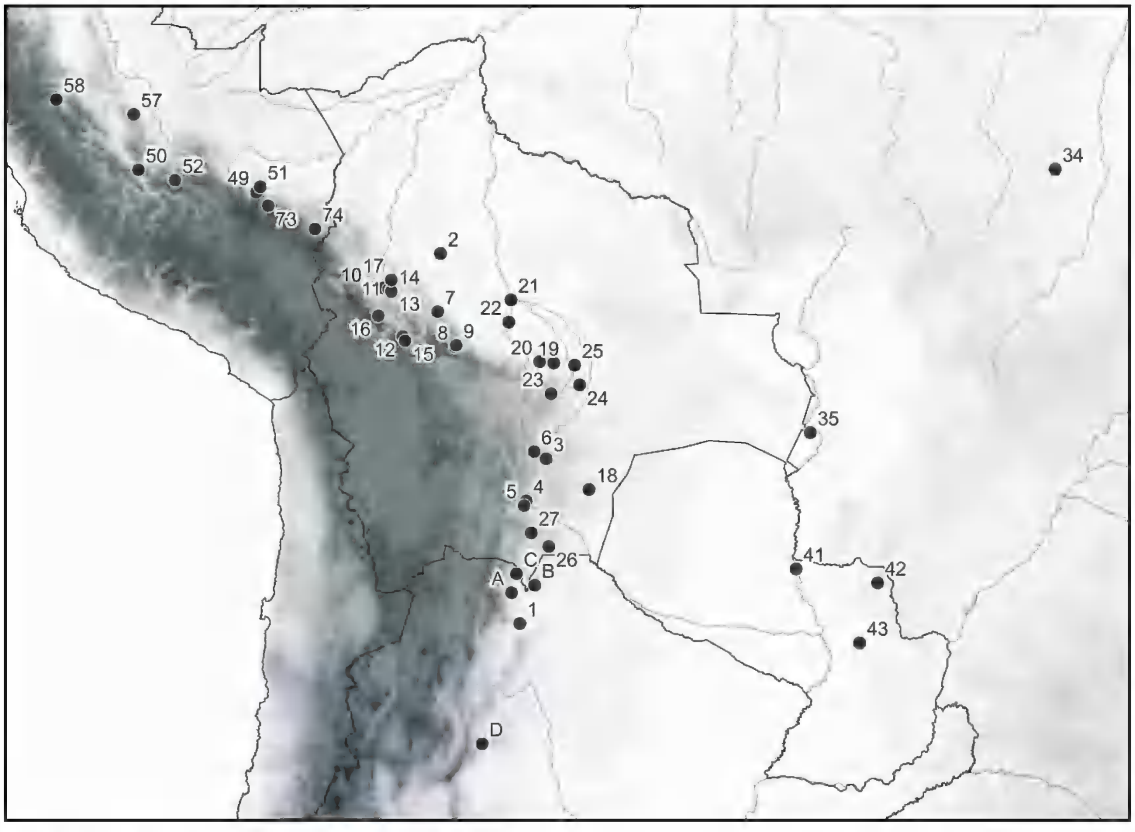


FIG. 12. Collection localities for examined specimens of *Marmosa rapposa*. Numbers are keyed to entries in gazetteer (appendix 2). Lettered localities correspond to selected Argentinian specimens examined by Silva et al. (2019) from Salta (A–C) and Tucumán (D).

brownish gray (near Ridgway's Light Brownish Olive), often slightly paler in lowland specimens than in specimens from montane habitats, but otherwise remarkably constant in coloration throughout the wide geographic distribution of the species. Fur length at mid back ranges from 8 to 16 mm, but most specimens have middorsal fur that is 10–12 mm long; in general, lowland specimens are shorter furred than highland material. By contrast with the tonal uniformity observed in the dorsal pelage, the ventral fur varies considerably in color, from pale yellow (resembling Ridgway's Cartridge Buff) to pinkish-orange (near Ochraceous Salmon), with yellowish hues predominating in lowland specimens and richer pigments primarily in highland material. A broad, continuous median streak of self-colored fur extends from the chin to the groin in most specimens (fig. 7), but at least some of the lateral fur is often gray based, and a few specimens (only 5% of those scored for this trait; table 5) have mostly gray-based ventral fur; the fur of the chin, throat, and groin, however, is always self-colored. The tail, usually about 130%–140% of head-and-body length, is covered with short fur for about 25 mm or less (usually <20 mm) at its base, and the naked part of the tail is almost always boldly marked or spotted with white distally (particolored). In a few specimens, as much as half of the unfurred distal part of the tail is white, but only the tip is white in many others, and a few specimens (mostly from the Andean foothills of eastern Bolivia) have all-dark tails. The manus and pes are covered dorsally with

TABLE 5

Qualitative Trait Frequencies for *Marmosa rapposa*

Self-colored ventral fur (N = 42)	
continuous from chin to groin:	40 (95%)
discontinuous (gray-based on abdomen):	2 (5%)
Tail coloration (N = 40)	
particolored (marked with white distally):	33 (82.5%)
all-dark:	7 (17.5%)
Maxillopalatine fenestrae (N = 40)	
extend from P3 to M3:	28 (70%)
extend from P3 to M2:	3 (7.5%)
extend from M1 to M3:	9 (22.5%)
Palatine fenestrae (N = 48)	
bilaterally present:	45 (94%)
unilaterally present:	2 (4%)
absent:	1 (2%)
Posterior cingulids (N = 40)	
distinct on m1–m3:	30 (75%)
distinct on m1 & m2 only:	4 (10%)
distinct on m2 only:	4 (10%)
distinct on m2 & m3 only:	1 (2.5%)
absent/indistinct:	1 (2.5%)

short, pale (usually yellowish) hairs in most specimens, but the metapodials are indistinctly darker in some individuals.

Mature adult skulls (fig. 13A, D) usually have short, wide rostrums; broadly flaring zygomatic arches; and distinct postorbital processes.[6] The maxillopalatine fenestrae are usually widely open (seldom reduced to narrow slits), and often extend posteriorly from the level of P3 to the level of M3. Palatine fenestrae are almost always present and well developed. The auditory bullae are usually smoothly globular; none that we examined are acutely pointed ventrally ("conical" sensu Tate, 1933). The upper molar series (LM) is usually short (8.0–8.5 mm), the first three upper molars (M1–M3) have long postprotocristae, and posterior cingulids are usually present on m1–m3.

VARIATION: Qualitative variation in selected morphological traits is summarized in table 5. With the exceptions noted above (fur pigmentation in lowland versus highland material), no geographic variation in qualitative phenotypic traits was observed, and specimens exhibiting rare traits for one character are not unusual in other respects. For example, the single specimen we examined that lacks posterior cingulids (CM 4947) has well-developed palatine fenestrae, maxillopalatine foramina that extend from P3 to M3, and a particolored tail. Therefore, such variation has the aspect of intraspecific polymorphism rather than taxonomic heterogeneity.

Morphometric variation in our adult material (table 6) is typical of that observed in homogeneous mammalian samples (e.g., with coeffi-

[6] These traits are less well developed in young adults, and a few adults (e.g., USNM 582111, from an isolated high-altitude site) have narrower skulls than usual.

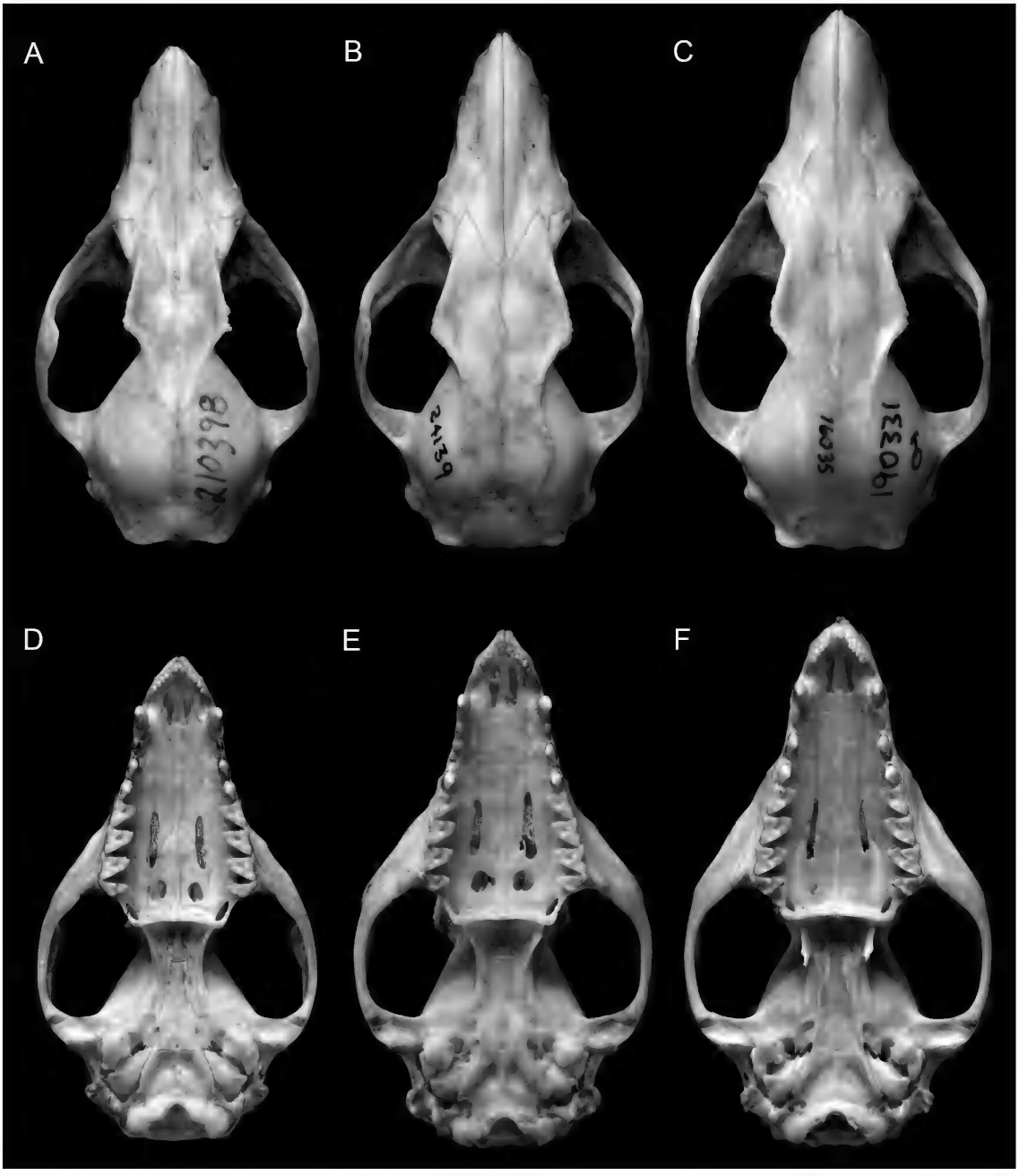


FIG. 13. Dorsal and ventral cranial views (×1.75) of *Marmosa rapposa* (**A**, **D**; AMNH 210398), *M. parda* (**B**, **E**; FMNH 24139), and *M. rutteri* (**C**, **F**; MVZ 190331). All specimens are adult males.

TABLE 6

Measurements (mm) and Weights (g) of *Marmosa rapposa*

	Males[a]	BMNH 20.1.7.134[b]	Females[c]	BMNH 98.11.6.13[d]
HBL	153 ± 17 (131–186) 15	"139"	150 ± 14 (118–170) 19	"195"
LT	213 ± 16 (180–239) 15	"186"	195 ± 19 (162–237) 19	"223"
HF	25 ± 2 (22–29) 17	26[e]	24 ± 2 (19–28) 23	29
Ear	26 ± 2 (23–30) 17	"22"	26 ± 2 (20–30) 18	"25"
CBL	39.7 ± 2.1 (36.2–44.2) 20	36.7	37.8 ± 2.2 (34.4–41.5) 20	45.6
NL	18.3 ± 1.1 (16.4–20.5) 19	16.3	17.2 ± 1.1 (15.3–18.7) 20	—
NB	5.2 ± 0.4 (4.8–6.1) 20	4.6	5.1 ± 0.4 (4.3–6.1) 25	6.2
LIB	7.1 ± 0.5 (6.3–8.6) 20	6.6	6.9 ± 0.6 (5.6–7.9) 25	8.9
LPB	6.9 ± 0.5 (6.2–7.7) 17	6.9	7.1 ± 0.4 (5.9–8.0) 24	7.7
ZB	22.6 ± 1.7 (20.2–26.1) 20	21.0	21.9 ± 1.6 (19.1–24.5) 24	24.8
PL	22.1 ± 0.9 (20.6–23.7) 20	20.7	21.3 ± 1.1 (19.4–23.0) 23	25.9
PB	13.0 ± 0.5 (12.0–13.8) 20	12.6	12.9 ± 0.6 (11.8–14.3) 25	14.4
MTR	16.1 ± 0.5 (15.2–16.9) 20	15.6	15.6 ± 0.4 (14.8–16.5) 26	18.1
LM	8.4 ± 0.2 (7.9–8.6) 20	8.6	8.3 ± 0.2 (8.0–9.0) 26	9.2
M1-3	7.1 ± 0.2 (6.7–7.3) 20	7.2	7.0 ± 0.2 (6.7–7.7) 26	7.7
WM3	2.8 ± 0.1 (2.6–2.9) 20	2.8	2.8 ± 0.1 (2.6–3.0) 26	2.8
Weight	81 ± 23 (52–132) 20	—	66 ± 19 (37–98) 18	—

[a] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for each measurement of the following series: AMNH 210398, 210399, 275464, 275466, 275468; CBF 14, 2332, 3569, 3570; MSB 6700, 70281, 70282, 140343, 140347, 140352; MVZ 172583; UMMZ 126676, 155910; USNM 390023, 390573.

[b] The subadult male holotype of *budini*. External measurements in scare quotes were not taken by the American method.

[c] The mean plus or minus one standard deviation, the observed range (in parentheses), and the sample size for each measurement of the following series: AMNH 63860–63863, 72569, 210400, 264923, 264924, 275463, 275465, 275467; BMNH 76.631; CBF 2334, 7551, 7556; FMNH 65678, 66411; MSB 59883, 63277, 87093, 140348, 140349, 140351, 140415; UMMZ 126678, 126679.

[d] The female holotype of *rapposa*. External measurements in scare quotes were not taken by the American method.

[e] Measured by R.S.V. on the dried hind foot.

cients of variation consistently <10 for craniodental dimensions; Yablokov, 1974). Although the holotype of *budini* (BMNH 20.1.7.134, from Argentina) is a subadult, it is only slightly smaller than our smallest measured adult specimens (from Bolivia, Brazil, Peru, and Paraguay) in two nasal dimensions. By contrast, the old adult female holotype of *rapposa* (BMNH 98.11.6.13) is substantially larger than any other specimen (of either sex) in several craniodental dimensions, but other specimens from Cuzco (e.g., FMNH 65678, 66411) have unremarkable measurements, and a large (518 bp) fragment of cytochrome *b* that we were able to amplify and sequence from dried tissue scraped from the holotype skull supports the application of *rapposa* to specimens that share the external and craniodental traits described above. Therefore, we conclude that the type is simply an unusually large specimen. Other odd attributes of the holotype include a discontinuous facial mask (dark mystacial and circumocular markings are separated by a narrow line of yellowish fur; Thomas, 1899b) and short postprotocristae. However,

TABLE 7

Selected Morphological Comparisons among Species of the Rapposa Group of *Marmosa* (*Micoureus*)

	M. rapposa	*M. parda*	*M. rutteri*
Ventral pelage	mostly self-colored	mostly gray-based	mostly self-colored
Tail	particolored (whitish distally)	all dark	all dark
Palatine fenestrae	present	present	absent
Length of molars[a]	8.3 ± 0.2 mm	8.8 ± 0.2 mm	9.0 ± 0.4 mm

[a] Crown length M1–M4 (see Materials and Methods). Table entries are the mean plus or minus one standard deviation computed from measurements of both sexes.

topotypical paratype skins have continuous facial masks, and the molars of the only preserved topotypical paratype skull (BMNH 98.11.6.14) have long postprotocristae. The problem of atypical holotypes is well known (Daston, 2004) and requires no additional comment here.

COMPARISONS: *Marmosa rapposa* differs from other members of the Rapposa Group in several characters (table 7). Whereas the ventral pelage of *M. rapposa* usually includes a broad midventral zone of self-colored fur (sometimes entirely without lateral zones of gray-based hairs), the ventral pelage of *M. parda* is almost entirely gray based (occasionally with a narrow median streak of self-yellow hairs), and the self-colored ventral fur of *M. rutteri* is usually narrowed by lateral zones of gray-based hairs and is sometimes discontinuous. Most (>80%) examined specimens of *M. rapposa* have tails that are marked with white ("depigmented" sensu Silva et al., 2019) distally, but all examined specimens of *M. parda* and *M. rutteri* have completely dark tails. According to Silva et al. (2019), specimens of *M. rapposa* (which they called *M. budini*) usually have more than three hairs emerging from the posterior edge of each caudal scale, whereas specimens of *M. rutteri* (which they called *M. regina*) usually have only three hairs per scale, but we did not score this character for our study.

Craniodental traits provide other diagnostic criteria. In general, skulls of *Marmosa rapposa* are less robust than those of *M. parda* and *M. rutteri*, and they tend to have smaller (but usually distinct) postorbital processes. A less subjective basis for sorting specimens is the palatine fenestrae, which are bilaterally present in >90% of the specimens we examined of *M. rapposa* and in all examined specimens of *M. parda*, but which are usually absent (or, when present, are much smaller) in *M. rutteri*. Lastly, the upper molar toothrow is substantially shorter, on average, in *M. rapposa* than in *M. parda* and *M. regina*.

REMARKS: We include several putative species identified by our mPTP analysis under this binomen (fig. 14). The haplogroup we call *rapposa* A consists of a single sequence from the Peruvian holotype, whereas *rapposa* B includes 17 sequences from widely scattered localities in Bolivia, Brazil, and Paraguay. A third haplogroup, *rapposa* C, includes two sequences from a single locality in the Cordillera Vilcabamba, an outlying spur of the Peruvian Andes. Sequence divergence between *rapposa* A and *rapposa* B is only about 3%, but *rapposa* C differs from the other haplogroups by about 7%–8% (table 4). Although the latter values are notably high for intraspecific sequence comparisons, we are unable to phenotypically distinguish specimens from the Cordillera Vilcabamba from other material of *M. rapposa*, so it seems best to treat all three haplogroups as conspecific in the absence of other evidence of lineage independence.

Specimens of *Marmosa rapposa* have long been misidentified as *M. constantiae* (e.g., by Tate, 1933; Anderson, 1997; Flores et al., 2007; Gardner and Creighton, 2008; Voss et al., 2009; de la Sancha et al., 2012). Indeed, the holotype (BMNH 3.7.7.157) and other specimens of *M.*

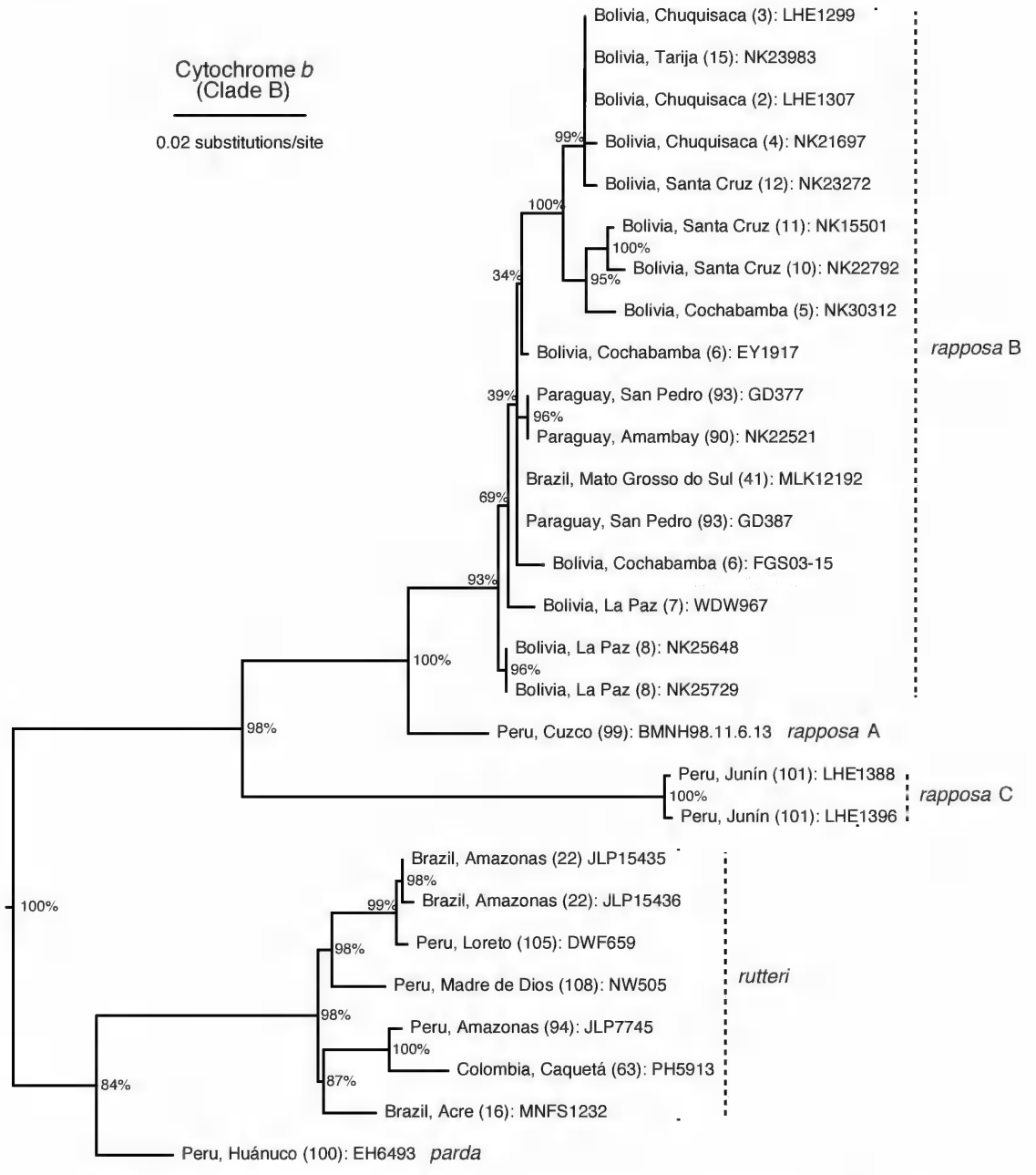


FIG. 14. Relationships among 28 cytochrome *b* sequences of species in the Rapposa Group. This subtree shows the full details of the cartooned lineages belonging to Clade B in figure 5

constantiae from eastern Bolivia (e.g., AMNH 209158–209162, 210397) and western Mato Grosso (AMNH 384, OMNH 37209) superficially resemble lowland material of *M. rapposa* by having a continuous median zone of self-yellow ventral fur and tails that are boldly marked with white. Externally, these species are difficult to tell apart where they occur together, although *M. constantiae* has a longer furry tail base (usually >25 mm). However, *M. constantiae* differs from *M. rapposa* in several craniodental traits, notably by lacking palatine fenestrae, by having short postprotocristae on M1–M3 (fig. 10), and by lacking any trace of posterior cingulids (fig. 11); additionally, *M. constantiae* has larger molars (LM = 8.7–9.2 mm) and bullae that tend to become distinctly conical in older adults.

For the last 25 years *Marmosa rapposa* has been treated as a synonym (Gardner, 1993) or subspecies (Gardner and Creighton, 2008) of *M. regina*, but there is no compelling evidence to support the hypothesis that these are closely related taxa. The type of *M. regina* (BMNH 98.5.15.4) consists of the skin and skull of an old adult male collected by G.D. Child in "W[est]. Cundinamarca (Bogotá region)" (Thomas, 1898: 275). As noted by Patton et al. (2000: 76), the type locality of *regina* is probably somewhere in the Río Magdalena valley of Colombia, which is separated from the rest of the enormous geographic range previously attributed to this species (Gardner and Creighton, 2008: map 35) by formidable elevations of the eastern Andean cordillera. Among other traits by which it differs from *M. rapposa*, the holotype of *M. regina* lacks palatine fenestrae and has distinctly redder dorsal fur (formerly near Prout's Brown according to Tate [1933: 83], who saw the type when it was less than 40 years old), a well-developed gular gland, an all-dark tail, and short postprotocristae. Like Tate (1933), Voss et al. (2019) restricted the application of *M. regina* to the holotype, which does not closely resemble any other specimen of *Micoureus* that we have examined.

In a well-executed and meticulously documented study of mtDNA sequence data and craniodental morphology, Silva et al. (2019) identified the present species as *Marmosa budini*, a name that we treat as a junior synonym. The holotype of *M. budini* (BMNH 20.1.7.134) consists of the skin and skull of a subadult[7] male collected by Emilio Budin on 23 July 1919 at 500 m on the Altura de Yuto near the Río San Francisco in the province of Jujuy, Argentina. Except for its slightly smaller nasal measurements (discussed above; see Variation), this specimen is morphologically indistinguishable from sequenced Bolivian material that clusters with the partial sequence we obtained from the type of *M. rapposa*.

One specimen of *Marmosa rapposa*—AMNH 72569, from Ñequejahuira at 8000 ft (2450 m) above sea level on the eastern slopes of the Cordillera Real of La Paz department, Bolivia—was part of Tate's (1931) type series of *M. mapiriensis*, but it is not conspecific with the holotype (AMNH 72555), which was collected in the adjacent foothills at Ticunhuaya (1500 m). Among other noteworthy differences from *M. rapposa*, AMNH 72555 lacks palatine fenestrae and posterior cingulids; additionally, it has short postprotocristae, short and narrow maxillopalatine fenestrae, and strongly conical auditory bullae. As noted earlier, we provisionally regard *mapiriensis* as a junior synonym of *M. constantiae*.

HABITATS: Explicit descriptions of habitats in which specimens of *Marmosa rapposa* have been collected are uncommon. Ecological maps suggest that most Andean specimens were collected in montane ("cloud") forest and that most lowland specimens were taken in dry forests, and these ecological associations are generally supported by brief notations on specimen tags and in field notes. According to Silva et al. (2019: 17), this species occurs in multiple ecoregions (sensu Olson et al., 2001) including "Cerrado, Chaco (savannic and humid), Pantanal, Parana/Paraíba interior forests, Bolivian Yungas, Andean Yun-

[7] Thomas (1920a: 196) described this specimen as "adult but not old," Tate (1933: 76) described it as a "young adult," and Jenkins and Knutson (1983: 15) described it as an "adult," but P3 is not quite fully erupted, so we consider it to be subadult.

FIG. 15. Habitat of *Marmosa rapposa* in ridge-top forest at about 1600 m in the Serranía Mosetenes, Cochabamba department, Bolivia (photo by Teresa Tarifa).

gas, south-western Amazonian moist forests, Chiquitania dry forests, and Bolivian montane dry forests," but their list conveys little about the appearance of vegetation in which the species is actually found because many of these ecoregions (e.g., the Cerrado; Eiten, 1972) are mosaics of quite different habitat types. Detailed descriptions of the vegetation at distant localities where *M. rapposa* have been collected are in Ratter et al. (1973) and Holst (1997), but carefully conducted trapping programs at sites like these would be necessary to establish which local habitats are "sinks" and which are "sources" (Pulliam, 1988) for this species.

Despite their very broad geographic overlap, the only place where *Marmosa rapposa* and *M. constantiae* are known to occur sympatrically is the Serranía (or Cordillera) Mosetenes in Cochabamba department, Bolivia (appendix 3: locality 7). In September 2003, Fernando Guerra, Teresa Tarifa, and Eric Yensen collected two specimens of *M. rapposa* (CBF 7551, 7556) and two specimens of *M. constantiae* (CBF 7515, 7540) in the Serranía Mosetenes at elevations ranging from 1200 to 1600 m. According to Tarifa et al. (2008), local habitats included bamboo thickets, regenerating montane forest, mature montane forest, and ridge forest; apparently, *M. constantiae* ("*Micoureus demerarae*") was captured only in montane forest, whereas *M. rapposa* ("*Mic. regina*") was captured in both montane forest and ridge forest. The ridge-forest habitat (figs. 15, 16) of *M. rapposa* was said to consist of stunted trees heavily laden with epiphytes, and to lack

FIG. 16. Interior of ridge-top forest in the Serranía Mosetenes, Cochabamba department, Bolivia (photo by Teresa Tarifa).

the "Amazonian elements" observed in mature montane forest.

SPECIMENS EXAMINED (N = 94): **Argentina**—*Jujuy,* Altura de Yuto (BMNH 20.1.7.134 [holotype of *budini*]). **Brazil**—*Mato Grosso,* 264 km N Xavantina (BMNH 76.631); *Mato Grosso do Sul,* 10 km NE Urucum (USNM 390023). **Bolivia**—*Beni,* 5 km N Estancia El Porvenir (CBF 14); *Chuquisaca,* 2 km E Chuyayacu (MSB 63276), El Limón (LHE 1307), Rinconada del Bufete (LHE 1299), Río Limón (MSB 63277); *Cochabamba,* Serranía Mosetenes (CBF 7551, 7556), 4.4 km N Tablas Monte (AMNH 264924, CBF 3570, MSB 70281), 9.5 km NE Tablas Monte (AMNH 264923, CBF 3569, MSB 70282); *La Paz,* 4 km NW Alcoche (UMMZ 126679, 127170), Cajuata (CBF 6606, 6607), 20 km NNE Caranavi (UMMZ 126676–126678, 127171), La Reserva (AMNH 275463–275465, 275467; MSB 140341–140345, 140347–140352, 140415), 1 km S La Reserva (CBF 2332, 2334); Los Molinos de Titiamaya (CBF 4996), Ñequejahuira (AMNH 72569), 1 mi W Puerto Linares (TTU 34785); *Santa Cruz,* 53 km E Boyuibe (AMNH 275466), Buenavista (CM 5049; FMNH 25266, 51902–51905), Cerro Hosane (CM 4941, 4947, 4951), 2 km N Chapare River mouth (AMNH 210398, 210399), 54 km S Chapare River mouth (AMNH 210400), 1 km NE Estancia Cuevas (MSB 67019), Río Surutú (CM 5040), 27 km SE Santa Cruz (MSB 59883), Warnes (USNM 390573); *Tarija,* 3 km WNW Carapari (AMNH 275468), 5 km NNW Entre Ríos (MSB 87093). **Paraguay**—*Alto Paraguay,* Puerto Casado (FMNH 54404); *Amambay,* Parque Nacional Cerro Cora (MSB 67000, UMMZ 134550); *San Pedro,* Ganadera La Carolina (UMMZ 174909, 174992). **Peru**—*Cusco,* Hacienda Cadena (FMNH 65678, 66411, 68330, 75102), Vilcanota River just north of Cuzco (BMNH 98.11.6.13 [holotype of *rapposa*], 98.11.6.14–98.11.6.17); *Junín,* "Camp Two" in Cordillera Vilcabamba (MUSM 13004, 13005; USNM 582111, 582112), 15 km by road SW San Ramón (UMMZ 155909–155911, 158013–158015), Utcuyacu (AMNH 63860–63863); *Puno,* 11 km NNE Ollachea (MVZ 172582), 14 km W Yanahuaya (MVZ 172583).

Marmosa (*Micoureus*) *parda* Tate, 1931

Marmosa germana parda Tate, 1931: 4 (original description).

Marmosa (*Marmosa*) *germana parda*: Cabrera, 1958: 15 (name combination).

Micoureus regina: Gardner, 1993: 20 (part; *parda* treated as synonym); not *regina* Thomas, 1898.

Micoureus regina germanus: Gardner and Creighton, 2008: 81 (part; *parda* treated as synonym); not *germana* Thomas, 1904.

Marmosa (*Micoureus*) *regina*: Voss and Jansa, 2009: 101 (part; *parda* treated as synonym); not *regina* Thomas, 1898.

TYPE MATERIAL AND TYPE LOCALITY: The holotype (by original designation, FMNH 24140) consists of the skin and skull of an adult male collected by J.T. Zimmer on 28 September 1922 at Huachipa, Huánuco, Peru. Both elements of the type specimen are in excellent condition. In addition to the holotype, Tate (1931) mentioned that he had examined 15 other specimens of this taxon, all of which can be considered paratypes; Tate (1933: 82–83) listed this material, which included several BMNH specimens, but not all of these are conspecific with the holotype (see Remarks, below).

DISTRIBUTION AND SYMPATRY: The material we refer to *Marmosa parda* is all from the upper Río Huallaga drainage between about 1000 and 2000 m in the departments of Huánuco and La Libertad, Peru (fig. 17). We are not aware that this species occurs sympatrically with any other member of the subgenus *Micoureus*.

DESCRIPTION: The dorsal pelage of *Marmosa parda* is dull brownish gray (near Ridgway's Citrine Drab or Grayish Olive), with little tonal variation in the material we examined; at midback the fur ranges in length from 12 to 15 mm. The ventral fur is almost completely gray based, except

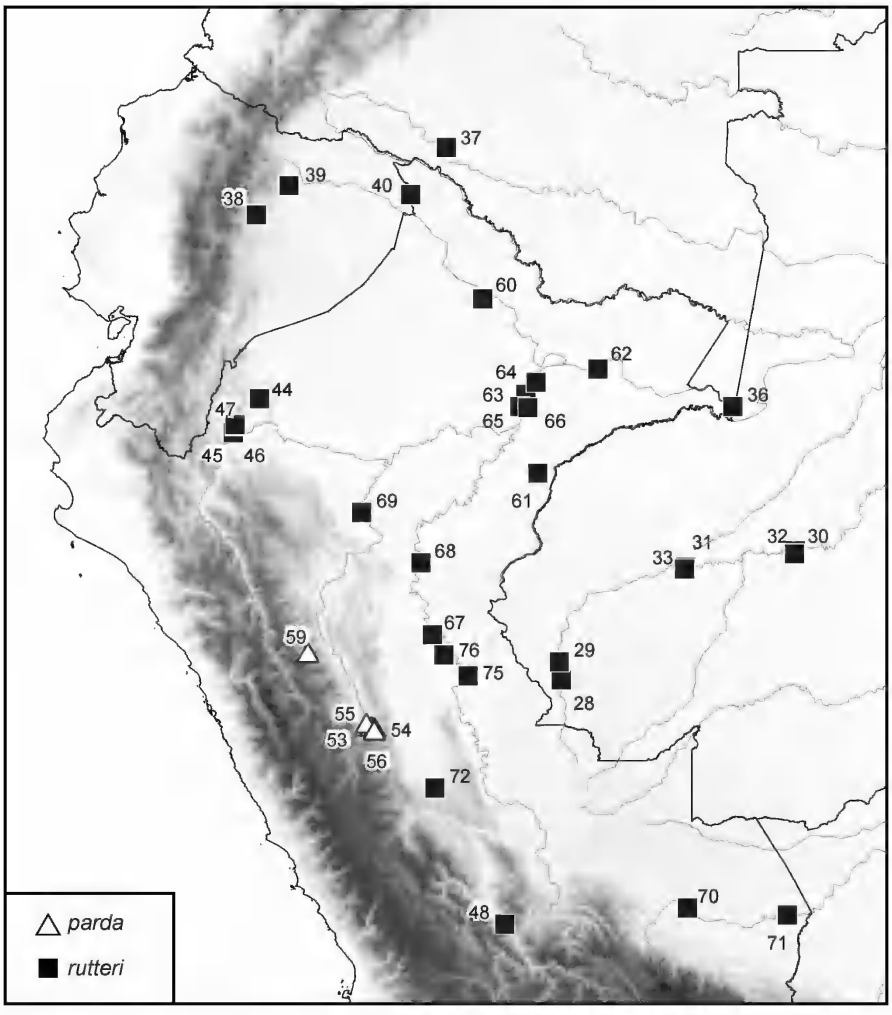


FIG. 17. Collection localities for examined specimens of *Marmosa parda* and *M. rutteri*. Numbers are keyed to entries in gazetteer (appendix 3).

on the chin and groin, which have self-yellowish or -buffy fur; additionally, a very narrow median streak of self-yellowish fur is present in some specimens. The tail seems to be slightly more than 130% of head-and-body length, judging from the few available specimens measured by the American method; it is covered with short fur for only about 25 mm or less at the base, and the exposed caudal skin is completely dark (brownish in dried specimens) without any bold whitish markings. The manus and pes are covered dorsally with pale hairs in most specimens, but a few have indistinctly darker metacarpal pelage.

Mature adult skulls of *Marmosa parda* are larger and more robust than those of *M. rapposa* in same-sex comparisons (fig. 13, table 8). However, these taxa are otherwise cranially similar, with short, wide rostrums; broadly flaring zygomatic arches; and well-developed postorbital processes. In ventral view, the maxillopalatine fenestrae are widely open and extend from M1 to M3 in most specimens. Palatine fenestrae are consistently present and usually well developed. The auditory bullae are smoothly globular in most specimens, but they are faintly conical in at least one (FMNH 24137), which has vascularized

TABLE 8

Measurements (mm) and Weights (g) of *Marmosa parda*

	FMNH 24139	FMNH 24140[a]	FMNH 24137	FMNH 24138	LSUMZ 22324	BMNH 27.11.1.246	BMNH 27.11.1.248
Sex	male	male	female	female	female	female	female
HBL	160[b]	171	147[b]	137[b]	177	159[b]	164[b]
LT	242[b]	235	223[b]	210[b]	225	266[b]	–
HF	28	28	"24"	26[c]	27[c]	27[c]	26[b]
Ear	–	–	–	–	26	24.5[b]	24[b]
CBL	43.6	43.6	41.6	40.0	41.1	40.6	–
NL	19.6	20.0	19.3	18.6	18.5	19.0	19.2
NB	6.2	7.0	6.5	5.8	6.0	6.5	6.2
LIB	8.7	8.9	8.2	7.9	8.1	8.0	8.0
LPB	8.0	8.7	8.1	7.9	8.3	7.8	7.5
ZB	25.4	24.8	24.1	23.4	22.6	23.1	23.0
PL	24.5	24.4	23.6	22.4	23.0	23.4	23.3
PB	14.1	13.8	13.4	14.2	13.7	14.0	14.9
MTR	16.7	17.7	16.4	16.5	16.8	17.0	17.0
LM	8.5	9.1	8.7	9.0	8.8	9.0	8.8
M1–3	7.2	7.5	7.4	7.6	7.2	7.4	7.3
WM3	2.7	2.7	2.9	2.8	2.9	2.9	3.0
Weight	–	–	–	–	82	–	–

[a] Holotype.
[b] Measured by the British method.
[c] Measured by R.S.V. from dried skin.

sinuses on the ventral apex. The upper molar series is longer than those typically seen in *M. rapposa*, ranging from 8.5 to 9.1 mm in the specimens we measured. The first three upper molars have long postprotocristae. Most specimens have distinct postcingulids on m1–3, but these structures are indistinct (possibly worn away) in two specimens (FMNH 24138, 24139).

Comparisons: Comparisons of *Marmosa parda* with *M. rapposa* have already been provided, so it only remains to compare this species with its sister taxon, *M. rutteri*. These species are externally similar, but the dorsal fur is typically somewhat longer in *parda* (≥12 mm) than in *rutteri* (in which it is usually <12 mm). Additionally, the tail appears to be relatively shorter in *parda* than in *rutteri*, although this is hard to assess with measurements obtained in the field by collectors using different protocols. Lastly, the ventral fur is more extensively gray based in most specimens of *parda* than it is in most specimens of *rutteri*. Although Tate (1933: 83) claimed that *parda* and *rutteri* were not distinguishable cranially, the clearest distinction between these taxa is the consistent, bilateral presence of large palatine fenestrae in *parda* and the absence, unilateral presence, or reduced size of these openings in *rutteri*.

Remarks: Tate (1931) originally described *Marmosa parda* as a subspecies of *M. germana*, but *M. germana* is a distantly related taxon (fig. 6) that has short postprotocristae

and lacks palatine fenestrae and postcingulids. Specimens that we refer to *M. germana* are only known from lowland localities north of the Amazon in northeastern Peru and eastern Ecuador.

Among the BMNH paratypes listed by Tate (1933: 82–83), only two that we examined (BMNH 27.11.1.246, 27.11.1.248), both from Huánuco, are conspecific with the holotype. The others, from Pasco (BMNH 12.1.15.8) and San Martín (BMNH 24.8.1.4, 27.1.1.174–27.1.1.176) are examples of *M. constantiae*, with longer, fluffier fur at the base of the tail and short postprotocristae; none has palatine fenestrae nor any trace of postcingulids on the lower molars.

HABITATS: Nothing has been recorded about the habitats occupied by this species, but the typical vegetation of the eastern Andean slopes of central Peru between about 1000 and 2000 m is premontane or montane rainforest.

SPECIMENS EXAMINED (N = 7): **Peru**—*Huánuco*, Chinchavita (BMNH 27.11.1.246, 27.11.1.248), Hacienda Porvenir (FMNH 24139), Hacienda San Antonio (FMNH 24137, 24138), Huachipa (FMNH 24140); *La Libertad*, on trail to Ongón (LSUMZ 22324).

Marmosa (*Micoureus*) *rutteri* Thomas, 1924

Marmosa rutteri Thomas, 1924: 536 (original description).

Marmosa germana rutteri: Tate, 1933: 81 (name combination).

Marmosa (*Marmosa*) *germana rutteri*: Cabrera, 1958: 15 (name combination).

Micoureus regina: Gardner, 1993: 20 (part; *rutteri* treated as synonym); not *regina* Thomas, 1898.

Micoureus regina germanus: Gardner and Creighton, 2008: 81 (part; *rutteri* treated as synonym); not *germana* Thomas, 1904.

Marmosa (*Micoureus*) *regina*: Voss and Jansa, 2009: 101 (part, *rutteri* treated as synonym); not *regina* Thomas, 1898.

TYPE MATERIAL: The holotype (by original designation, BMNH 24.2.22.67) consists of the skin and skull of an adult male collected by Latham Rutter on 10 September 1923 at "Tushemo, near Masisea" at an elevation of 1000 ft [305 m] in the Peruvian department of Ucayali.

DISTRIBUTION AND SYMPATRY: *Marmosa rutteri* is a lowland Amazonian species that has been collected at or below about 800 m in southeastern Colombia, eastern Ecuador, eastern Peru, and western Brazil. It is known to occur sympatrically with several other members of the subgenus *Micoureus*, including *M. constantiae* (south of the Amazon in western Brazil and eastern Peru), *M. germana* (north of the Amazon in eastern Peru and eastern Ecuador), and an undescribed species (*M.* "Yasuni"; see above) that appears to have much the same geographic distribution as *M. germana*.

DESCRIPTION: The dorsal pelage of *Marmosa rutteri* ranges in color from a dull grayish hue (near Ridgway's Deep Grayish Olive) to paler, more yellowish tones (close to Light Brownish Olive or even to Isabella Color); at midback the fur ranges in length from 8 to 16 mm, with longer fur typically in foothill material, but in most specimens we measured the middorsal fur is 9–11 mm long. The ventral pelage, at least along the midline from chin to groin, is usually self-yellowish (e.g., Antimony Yellow or Colonial Buff), although there are often broad lateral zones of gray-based fur on the lower thorax and abdomen (between the fore- and hind limbs), and a few skins have mostly gray-based ventral fur with self-yellowish fur only on the chin, throat, and groin. The tail is approximately 145% of head-and-body length, on average, and only a short part of the base (usually <20 mm) is covered with fur; the naked, scaly part of the tail is completely dark (grayish or grayish brown in life), and it is not marked with white in any specimen that we examined.

Adult skulls (fig. 13C, F) have short, wide rostrums and broadly flaring zygomatic arches. The postorbital processes, even of most young adults, are large and triangular. The maxillo-

TABLE 9

Measurements (mm) and Weights (g) of *Marmosa rutteri*

	BMNH 24.2.22.67[a]	Males[b]	Females[c]
HBL	158[d]	184 ± 11 (164–203) 17	174 ± 16 (152–206) 15
LT	213[d]	260 ± 17 (227–291) 17	240 ± 16 (210–269) 15
HF	28[d]	29 ± 2 (25–33) 18	28 ± 2 (25–30) 18
Ear	23[d]	26 ± 2 (23–29) 18	25 ± 1 (23–28) 17
CBL	—	45.0 ± 2.0 (41.6–49.7) 25	42.7 ± 2.0 (39.6–46.5) 24
NL	18.1	20.2 ± 1.5 (17.4–23.0) 29	19.2 ± 1.2 (17.2–21.6) 20
NB	5.6	6.4 ± 0.6 (5.5–7.7) 32	6.1 ± 0.5 (4.8–6.9) 26
LIB	7.3	8.4 ± 0.6 (7.2–9.6) 31	8.0 ± 0.5 (7.3–9.2) 26
LPB	7.2	7.4 ± 0.6 (5.9–8.6) 31	7.4 ± 0.6 (6.4–8.2) 26
ZB	—	25.8 ± 1.5 (23.4–28.7) 28	24.6 ± 1.3 (22.4–27.4) 25
PL	22.8	25.0 ± 1.2 (22.5–27.6) 31	24.0 ± 1.0 (22.2–26.6) 25
PB	13.3	14.5 ± 0.7 (13.1–15.7) 29	14.4 ± 0.6 (13.4–16.2) 26
MTR	16.7	17.9 ± 0.8 (16.7–19.4) 31	17.5 ± 0.6 (16.7–18.8) 26
LM	8.6	9.0 ± 0.4 (8.3–9.8) 31	9.1 ± 0.3 (8.6–9.6) 26
M1–3	7.3	7.6 ± 0.3 (7.0–8.2) 32	7.7 ± 0.2 (7.2–8.1) 26
WM3	2.9	3.0 ± 0.2 (2.6–3.3) 32	3.0 ± 0.1 (2.7–3.2) 26
Weight	—	132 ± 30 (84–180) 17	105 ± 23 (63–151) 12

[a] Holotype.

[b] The sample mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size based on measurements of the following series: AMNH 71958, 76302, 230021; BMNH 24.2.22.67, 28.5.2.231–28.5.2.235, 28.5.2.237, 28.5.2.240; FMNH 46110, 46111; KU 144110; MUSM 11055, 11063, 15316; MVZ 154749, 154755, 154762, 154764, 154766, 157629, 157630, 157631, 190319, 190320, 190323, 190329–190332.

[c] The sample mean plus or minus one standard deviation, the observed range (in parentheses) and the sample size based on measurements of the following series: AMNH 71951, 72009, 72010, 74087, 98655, 98712, 273164; BMNH 28.5.2.241; FMNH 19635, 55467, 70966, 75100, 87118, 124613; KU 144093, 144095, 144100, 144102, 144107; LSMUZ 15674; MUSM 6086, 6087; MVZ 154758, 157628, 190321, 190326.

[d] Measured by the British method.

palatine fenestrae extend from the level of M1 to the level of M3 in most specimens, but in many others they extend only from M1 to M2; however, these openings are seldom very wide, usually taking the form of narrow, bilaterally paired slits. Palatine fenestrae are bilaterally absent in most specimens, but small openings in the posterior palate are present unilaterally (e.g., in fig. 13F) and sometimes bilaterally in others. The first three upper molars (M1–M3) have long postprotocristae, and posterior cingulids are often distinct on m1–m3 (but always, at least, on unworn m2).

VARIATION: Summary statistics for external and craniodental measurements of *Marmosa rutteri* are provided in table 9, and qualitative trait variation is summarized in table 10. None of the morphometric or qualitative variation in this species seems particularly noteworthy, nor does this variability appear to be geographically structured. For example, we observed broad morphometric overlap between samples collected north and south of the upper Amazon. Although a few populations exhibit high frequencies of unusual phenotypes (e.g., 6 out of 10 specimens that we scored for ventral fur color from Amazonas

TABLE 10

Qualitative Trait Frequencies for *Marmosa rutteri*

Self-colored ventral fur (N = 52)	
continuous from chin to groin:	42 (81%)
discontinuous (gray-based on abdomen):	10 (19%)
Tail coloration (N = 50)	
particolored (marked with white distally):	0 (0%)
all-dark:	50 (100%)
Maxillopalatine fenestrae (N = 55)	
extend from P3 to M3:	1 (2%)
extend from P3 to M2:	1 (2%)
extend from M1 to M3:	39 (71%)
extend from M1 to M2:	13 (24%)
absent:	1 (2%)
Palatine fenestrae (N = 53)	
bilaterally present:	7 (13%)
unilaterally present:	10 (19%)
absent:	36 (68%)
Posterior cingulids (N = 47)	
distinct on m1–m3:	21 (45%)
distinct on m1 & m2 only:	10 (21%)
distinct on m2 only:	13 (28%)
absent/indistinct:	3 (6%)

department, Peru, had mostly gray-based ventral fur), we interpret these as evidence of geographic variation in a single, widespread species.

Comparisons: Comparisons of *Marmosa rutteri* with other members of the Rapposa Group are provided in the preceding accounts. *Marmosa rutteri* differs from other (non-Rapposa Group) species of the subgenus *Micoureus* with which it is sometimes sympatric (e.g., *M. constantiae* and *M. germana*) by its long postprotocristae on M1–M3, and by the presence of posterior cingulids on unworn m2 (and sometimes other lower molars); it is also substantially larger than the undescribed species of the Perplexa Group with which it co-occurs north of the Amazon (*M. "regina"* sensu Hice and Velazco, 2012). Additional comparisons between *M. rutteri* and *M. constantiae* were summarized by Voss et al. (2019: 27–29).

Habitats: The entire known geographic range of *Marmosa rutteri* is in western Amazonia, where the predominant natural climax vegetation is lowland rainforest. However, Amazonian vegetation is notoriously heterogeneous, including numerous distinct kinds of habitats, especially in riparian landscapes (Prance, 1979; Pires and Prance, 1985; Puhakka and Kalliola, 1995). Given that several species of the subgenus *Micoureus* have overlapping distributions in this region (see Distribution and sympatry, above), it would be reasonable to expect that some of them might be habitat specialists.

The most compelling evidence for habitat specialization by Amazonian species of *Marmosa* comes from an exemplary trapping study along the Rio Juruá in western Brazil (Patton et al., 2000). At numerous sites along this major white-

FIG. 18. Seasonally flooded forest (*várzea*) at Seringal Condor, on the left bank of the Rio Juruá, Amazonas state, Brazil (appendix 1: locality 25; photo by J.L. Patton). Sparse understory vegetation characterizes some *várzea* sites like this one, but dense stands of giant herbs such as *Heliconia* spp. (Heliconiaceae) and *Costa* spp. (Costaceae) can be common elsewhere (Prance, 1979).

water river, *Marmosa rutteri* ("*Micoureus regina*") and *M. constantiae* ("*Micoureus demerarae*") were found to occur sympatrically, although usually not syntopically. Equal numbers of both species (N = 55 each) were collected. Of these, specimens of *M. rutteri* were trapped in both *várzea* (seasonally flooded forest; fig. 18) and terra firme (unflooded) habitats, whereas *M. constantiae* was taken almost exclusively in terra firme (unflooded) forest.

A similar pattern of habitat segregation is suggested by less extensive trapping results from Cuzco Amazónico on the left (north) bank of the Río Madre de Dios, another major whitewater river, in southeastern Peru (appendix 3: locality 71). Here, *M. rutteri* was taken in approximately equal numbers in both terra firme forest and in seasonally flooded vegetation, whereas most specimens of *M. constantiae* were taken in terra firme forest (table 11). Based on these results, it seems plausible that *M. rutteri* might be a *várzea* specialist or, at least, might utilize seasonally flooded habitats to a greater extent than sympatric congeners.[8]

The same two field studies also provide the best available data about microhabitat occupancy by *Marmosa rutteri*. In Patton et al.'s (2000) study, substantial numbers of traps were set on the ground and in trees at each sampled site along the Rio Juruá; all of the 55 specimens of *M. rutteri* they collected were taken in arboreal traps

[8] In the commonly accepted terminology for Amazonian riparian vegetation (Prance, 1979), *várzea* refers to forests seasonally flooded by sediment-bearing (white-water) rivers, whereas *igapó* refers to forests seasonally flooded by sediment-free black- or clear-water rivers.

TABLE 11

Habitat Occupancy by Sympatric Species of *Marmosa* (*Micoureus*) at Cuzco Amazónico in Southeastern Peru
(Table entries are numbers of specimens trapped.)

	M. constantiae[a]	*M. rutteri*[a]	Totals
Zone 1[b]	5	6	11
Zone 2[c]	1	7	8
Totals	6	13	19

[a] Both species identified as "*Micoureus regina*" by Woodman et al. (1991, 1995). Only specimens that we examined are included in these counts.
[b] Trapping area located in terra firme forest (Duellman and Koechlin, 1991).
[c] Trapping area located in seasonally flooded forest (Duellman and Koechlin, 1991).

set 5–10 m above the ground, or were shot from arboreal perches >2 m above ground level. At Cuzco Amazónico, 20 out of 24 specimens of *M. rutteri* (ca. 83%) were trapped in trees (Woodman et al., 1995). These results are consistent with the commonly accepted notion that species of *Marmosa* are predominantly arboreal (Charles-Dominique et al., 1981; Miles et al., 1981; Vieira and Monteiro-Filho, 2003).

Specimens examined (N = 98): **Brazil**—*Acre,* Igarapé Porongaba (MVZ 190332), Nova Vida (MVZ 190333); *Amazonas,* Boa Esperança (MVZ 190330, 190331), Igarapé Nova Empresa (MVZ 190321, 190323–190325), opposite Altamira (MVZ 190328, 190329), Penedo (MVZ 190319, 190320), Seringal Condor (MVZ 190326). **Colombia**—*Amazonas,* Leticia (USNM 536890); *Caquetá,* Tres Troncos (FMNH 70964–70966). **Ecuador**—*Napo,* "near the river Napo" (BMNH 34.9.10.234–34.9.10.237); *Orellana,* San José de Payamino (FMNH 124613); *Sucumbíos,* Boca Río Lagartococha (AMNH 72008, 72009). **Peru**—*Amazonas,* La Poza (MVZ 157629), mouth of Río Cenepa (AMNH 98712), vicinity of Huampami (MVZ 153278, 154749, 154751, 154755, 154758, 154762, 154764, 154766, 157628, 157630, 157631), vicinity of Kayamas (MVZ 153281); *Ayacucho,* Santa Rosa on Río Santa Rosa (LSUMZ 15674); *Cuzco,* Quincemil (FMNH 75100); *Loreto,* Boca Río Curaray (AMNH 71951, 71956, 71958, 71964, 71966, 71968, 71975, 72010), Nuevo San Juan (AMNH 273164; MUSM 11055, 11063, 15315, 15316), Orosa (AMNH 74087), Otorongo (MUSM 33443), Pampa Chica (FMNH 87118), San Antonio (AMNH 98655), San Jerónimo (BMNH 28.5.2.231–28.5.2.241; FMNH 46110, 46111), Sarayacu (AMNH 76302, 76303), "Triunfo Chacras" (TTU 124799), Yurimaguas (FMNH 19635); *Madre de Dios,* Blanquillo (MUSM 8399), Reserva Cuzco Amazónico (KU 144091, 144093, 144095, 144100, 144102, 144107, 144110, 144111; MUSM 6083, 6086–6088, 6090–6092, 6100, 6101), 30 km above mouth of Río Tambopata (USNM 530907); *Pasco,* San Pablo (AMNH 230019, 230021); *Ucayali,* Tushemo (BMNH 24.2.22.67 [holotype]), Yarinacocha (FMNH 55467).

ACKNOWLEDGMENTS

Our research would not have been possible without the generous cooperation of colleagues at numerous museums (listed in Materials and Methods), who made dozens of specimens available to us on loan, or who hosted our visits to examine types and other material, especially Roberto Portela (at the BMNH); Bruce Patterson and John Phelps (FMNH); Robert M. Timm (KU); Jake Esselstyn and Steve Cardiff (LSUMZ); Joseph Cook and Jonathan Dunnum (MSB); Victor Pacheco and Judith Carrasco (MUSM); Jim Patton and Chris Conroy (MVZ); Burton Lim and Jacqui Miller (ROM); Robert Bradley and

Heath Garner (TTU); and Darrin Lunde and Nicole Edmison (USNM).

Our work was funded in part by National Science Foundation grants to R.S.V. (DEB-0743039) and S.A.J. (DEB-0743062). Research at the AMNH was made possible by the combined efforts of Eleanor Hoeger, Sara Ketelsen, and Marisa Surovy, who processed numerous specimen loans for this project. Patricia Wynne drew figures 4, 9, 10, and 11 with her customary skill and professionalism. Craig Chesek produced the skin photos (figs. 7 and 8), and Nicole Wong photographed the skulls (fig. 13). Morgan Hill took the SEM images from which Patricia Wynne subsequently drew figures 10 and 11. We thank Lorissa Fujishin for her careful lab work and expert databasing skills at the University of Minnesota.

We are grateful to Francisca Almeida, Cibele Bonvicino, Francois Catzeflis, João Oliveira, Jim Patton, Teresa Tarifa, Bob Timm, and Eric Yensen for providing geographic coordinates, field numbers, habitat descriptions, habitat photos, and other essential information about collected specimens. The image in figure 18 is reproduced with the permission of the Museum of Vertebrate Zoology, University of California, Berkeley. François Catzeflis and Alfred Gardner kindly read the submitted draft of our manuscript and offered helpful suggestions that improved the final text.

REFERENCES

Agrizzi, J., et al. 2012. Molecular diagnosis of Atlantic Forest mammals using mitochondrial DNA sequences: didelphid marsupials. Open Zoology Journal 5 (suppl. 1-M2): 2–9.

Allen, J.A. 1900. Note on the generic names *Didelphis* and *Philander*. Bulletin of the American Museum of Natural History 13 (15): 185–190.

Alonso, L.E., A. Alonso, T.S. Schulenberg, and F. Dallmeir (editors). 2001. Biological and social assessments of the Cordillera de Vilcabamba, Peru. RAP Working Papers 12: 1–257.

Anderson, S. 1997. Mammals of Bolivia, taxonomy and distribution. Bulletin of the American Museum of Natural History 231: 1–652.

Anthony, H.E. 1922. Preliminary report on Ecuadorean mammals. No. 2. American Museum Novitates 32: 1–6, map.

Apanaskevich, D.A., L.G. Domínguez, S.S. Torres, J.A. Bernal, V.M. Montenegro, and S.E. Bermúdez. 2017. First description of the male and redescription of the female of *Ixodes tapirus* Kohls, 1956 (Acari: Ixodidae), a parasite of tapirs (Perissodactyla: Tapiridae) from the mountains of Colombia, Costa Rica, and Panama. Systematic Parasitology 94: 413–422.

Bonvicino, C.R., V. Penna-Firme, and E. Braggio. 2002. Molecular and karyologic evidence of the taxonomic status of *Coendou* and *Sphiggurus* (Rodentia: Hystricognathi). Journal of Mammalogy 83: 1071–1076.

Byles, B., F. Catzeflis, R.P. Scheibel, and F.A. Jiménez. 2013. Gastrointestinal helminths of two species of mouse opossums (*Marmosa demerarae* and *Marmosa murina*) from French Guiana. Comparative Parasitology 80: 210–216.

Cabrera, A. 1958 ("1957"). Catálogo de los mamíferos de América del Sur [part 1]. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (Ciencias Zoológicas) 4 (1): i–iv, 1–307.

Carrara, L.A., L.C.P. Faria, F.I. Garcia, and P.T.Z. Antas. 2013. Avifauna da Estação Ecológica Estadual de Acauã e chapadas do alto vale do rio Jequitinhonha: ecótono de três biomas em Minas Gerais. Ornithologia 5 (2): 58–77.

Carstens, B.C., T.A. Pelletier, N.M. Reid, and J.D. Satler. 2013. How to fail at species delimitation. Molecular Ecology 22: 4369–4383.

Ceballos-Bendezú, I. 1981. Los mamíferos colectados en el Cusco por Otto Garlepp. Boletín de Lima 16–18: 108–119.

Charles-Dominique, P., et al. 1981. Les mammifères frugivores arboricoles nocturnes d'une forêt guyanaise: inter-relations plantes-animaux. Revue d'Ecologie (La Terre et la Vie) 35: 341–435.

Chernomor, O., A. von Haeseler, and B.Q. Minh. 2016. Terrace aware data structure for phylogenomic inference from supermatrices. Systematic Biology 65: 997–1008.

Clark, K.L., R.O. Lawton, and P.R. Butler. 2000. The physical environment. *In* N.M. Nadkarni and N.T. Wheelwright (editors), Monteverde: ecology and conservation of a tropical cloud forest: 15–38. New York: Oxford University Press.

Costa, L.P., Y.L.R. Leite, and J.L. Patton. 2003. Phylogeography and systematic notes on two species of gracile mouse opossums, genus *Gracilinanus* (Mar-

supialia: Didelphidae) from Brazil. Proceedings of the Biological Society of Washington 116: 275–292.

Daston, L. 2004. Type specimens and scientific memory. Critical Inquiry 31: 153–182.

de la Sancha et al., N.U., G. D'Elía, and P. Teta. 2012. Systematics of the subgenus of mouse opossums *Marmosa* (*Micoureus*) (Didelphimorphia, Didelphidae) with noteworthy records from Paraguay. Mammalian Biology 77: 229–236.

Dias, I.M.G., F.C. Almeida, G. Amato, R. DeSalle, and C.G. Fonseca. 2010. Delineating geographic boundaries of the woolly mouse opossums, *Micoureus demerarae* and *Micoureus paraguayana* (Didelphimorphia: Didelphidae). Conservation Genetics 11: 1579–1585.

Dirksen, L., and I. De la Riva. 1999. The lizards and amphisbaenians of Bolivia (Reptilia, Squamata): checklist, localities, and bibliography. Graellsia 55: 199–215.

Dmitriev, D.A., and R.A. Rakitov. 2008. Decoding of superimposed traces produced by direct sequencing of heterozygous indels. PLoS Computational Biology 7 (7): e1000113.

Duellman, W.E., and J.E. Koechlin. 1991. The Reserva Cuzco Amazónico, Peru: biological investigations, conservation, and ecotourism. Occasional Papers Museum of Natural History University of Kansas 142: 1–38.

Duellman, W.E., and J.R. Mendelson III. 1995. Amphibians and reptiles from northern Departamento Loreto, Peru: taxonomy and biogeography. University of Kansas Science Bulletin 55: 329–376.

Edgar, R.C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32: 1792–1797.

Eiten, G. 1972. The Cerrado vegetation of Brazil. Botanical Review 38: 201–341.

Emmons, L.H. 1998. Mammal fauna of Parque Nacional Noel Kempff Mercado. *In* T.J. Killeen and T.S. Schulenberg (editors), A biological assessment of Parque Nacional Noel Kempff Mercado, Bolivia (RAP Working Papers 10): 129–135. Washington, DC: Conservation International.

Flores, D.A., M.M. Díaz, and R.M. Barquez. 2007. Systematics and distribution of marsupials in Argentina: a review. University of California Publications in Zoology 134: 579–669.

Gardner, A.L. 1993. Order Didelphimorphia. *In* D.E. Wilson and D.M. Reeder (editors), Mammal species of the world, 2nd ed.: 15–23. Washington, DC: Smithsonian Institution Press.

Gardner, A.L. 2005. Order Didelphimorphia. *In* D.E. Wilson and D.M. Reeder (editors), Mammal species of the world, a taxonomic and geographic reference, 3rd ed.: 3–18. Baltimore: Johns Hopkins University Press.

Gardner, A.L. 2008 ("2007"). Mammals of South America, vol. 1: Marsupials, xenarthrans, shrews, and bats. Chicago: University of Chicago Press.

Gardner, A.L., and G.K. Creighton. 2008 ("2007"). Genus *Micoureus* Lesson, 1842. *In* A.L. Gardner (editor), Mammals of South America, vol. 1. (Marsupials, xenarthrans, shrews, and bats): 74–82. Chicago: Chicago University Press.

Giarla, T.C., R.S. Voss, and S.A. Jansa. 2010. Species limits and phylogenetic relationships in the didelphid marsupial genus *Thylamys* based on mitochondrial DNA sequences and morphology. Bulletin of the American Museum of Natural History 346: 1–67.

Giarla, T.C., R.S. Voss, and S.A. Jansa. 2014. Hidden diversity in the Andes: comparison of species delimitation methods in montane marsupials. Molecular Phylogenetics and Evolution 70: 137–151.

Gutiérrez, E.E., S.A. Jansa, and R.S. Voss. 2010. Molecular systematics of mouse opossums (Didelphidae: Marmosa): assessing species limits using mitochondrial DNA sequences, with comments on phylogenetic relationships and biogeography. American Museum Novitates 3692: 1–22.

Hall, E.R. 1962. Collecting and preparing study specimens of vertebrates. Miscellaneous Publications of the University of Kansas Museum of Natural History 30: 1–46.

Hershkovitz, P. 1977. Living New World monkeys (Platyrrhini), with an introduction to Primates (vol. 1). Chicago: University of Chicago Press.

Hice, C.L., and P.M. Velazco. 2012. The non-volant mammals of the Reserva Nacional Allpahuayo-Mishana, Loreto, Peru. Special Publications of the Museum of Texas Tech University 60: 1–135.

Hoang, D.T., O. Chernomor, A. Von Haeseler, B.Q. Minh, and L.S. Vinh. 2017. UFBoot2: Improving the ultrafast bootstrap approximation. Molecular Biology and Evolution 35: 518–522.

Holst, B.K. 1997. Vegetation of Tucumano-Boliviano forests in Chuquisaca, Bolivia. *In* T.S. Schulenberg and K. Awbrey (editors), A rapid assessment of the humid forests of south-central Chuquisaca, Bolivia (RAP Working Papers 8): 21–29. Washington, DC: Conservation International.

Hurtado, N., E. Arias, and V. Pacheco. 2014. Redescription of *Mimon koepckeae* (Chiroptera: Phyllostomidae). Zoologia 31: 377–388.

ICZN, 1999. International Code of Zoological Nomenclature, 4th ed. London: International Commission on Zoological Nomenclature.

Jenkins, P.D., and L. Knutson. 1983. A catalogue of the type specimens of Monotremata and Marsupialia in the British Museum (Natural History). London: British Museum (Natural History).

Jiménez, F.A., F. Catzeflis, and S.L. Gardner. 2011. Structure of parasite component communities of didelphid marsupials: insights from a comparative study. Journal of Parasitology 97: 779–787.

Kalyaanamoorthy, S., B.Q. Minh, T.K. Wong, A. von Haeseler, and L.S. Jermiin. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. Nature Methods 14 (6): 587.

Kapli, P., et al. 2017. Multi-rate Poisson tree processes for single-locus species delimitation under maximum likelihood and Markov chain Monte Carlo. Bioinformatics 33: 1630–1638.

Kearse, M. et al. 2012. Genious Basic: an integrated and expandable desktop software program for the organization and analysis of sequence data. Bioinformatics 28: 1647–1649.

Lanfear, R., P.B. Frandsen, A.M. Wright, T. Senfeld, and B. Calcott, B. 2016. PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Molecular Biology and Evolution 34: 772–773.

Langguth, A., V.L.A.G. Limeira, and S. Franco. 1997. Novo catálogo do material-tipo da coleção de mamíferos do Museu Nacional. Publicações Avulsas do Museu Nacional 70: 1–29.

Miles, M.A., A.A. de Souza, and M.M. Póvoa. 1981. Mammal tracking and nest location in Brazilian forest with an improved spool-and-line device. Journal of Zoology London 195: 331–347.

Miranda-Ribeiro, A. de. 1936. Didelphia ou Mammalia-Ovovivipara. Revista de Museu Paulista 20: 245–424.

Mitchell, K.J., et al. 2014. Molecular phylogeny, biogeography, and habitat preference evolution of marsupials. Molecular Biology and Evolution 31: 2322–2330.

Nguyen, L.T., H.A. Schmidt, A. von Haeseler, and B.Q. Minh. 2014. IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Molecular Biology and Evolution 32: 268–274.

Olson, D.M., et al. 2001. Terrestrial ecoregions of the world: a new map of life on earth. BioScience 51: 933–938.

Patton, J.L., and L.P. Costa. 2003. Molecular phylogeography and species limits in rainforest didelphid marsupials of South America. *In* M.E. Jones, C.R. Dickman, and M. Archer (editors), Predators with pouches: the biology of carnivorous marsupials: 63–81. Melbourne: CSIRO Press.

Patton, J.L., B. Berlin, and E.A. Berlin. 1982. Aboriginal perspectives of a mammal community in Amazonian Peru: knowledge and utilization patterns among the Aguaruna Jivaro. *In* M.A. Mares and H.H. Genoways (editors), Mammalian Biology in South America: 111–128. Pittsburgh: Pymatuning Laboratory of Ecology.

Patton, J.L., S.F. dos Reis, and M.N.F. da Silva. 1996. Relationships among didelphid marsupials based on sequence variation in the mitochondrial cytochrome *b* gene. Journal of Mammalian Evolution 3: 3–29.

Patton, J.L., M.N.F. da Silva, and J.R. Malcolm. 2000. Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. Bulletin of the American Museum of Natural History 244: 1–306.

Patton, J.L., U.F.J. Pardiñas, and G. D'Elía. 2015. Mammals of South America, vol. 2: Rodents. Chicago: University of Chicago Press.

Pavan, S.E., S.A. Jansa, and R.S. Voss. 2014. Molecular phylogeny of short-tailed opossums (Didelphidae: *Monodelphis*): taxonomic implications and tests of evolutionary hypotheses. Molecular Phylogenetics and Evolution 79: 199–214.

Paynter, R.A., Jr. 1989. Ornithological gazetteer of Paraguay, 2nd ed. Cambridge, MA: Museum of Comparative Zoology (Harvard University).

Paynter, R.A., Jr. 1992. Ornithological gazetteer of Bolivia, 2nd ed. Cambridge, MA: Museum of Comparative Zoology (Harvard University).

Paynter, R.A., Jr. 1993. Ornithological gazetteer of Ecuador, 2nd ed. Cambridge, MA: Museum of Comparative Zoology (Harvard University).

Paynter, R.A., Jr. 1997. Ornithological gazetteer of Colombia, 2nd ed. Cambridge, MA: Museum of Comparative Zoology (Harvard University).

Paynter, R.A., Jr., and M.L. Traylor, Jr. 1991. Ornithological gazetteer of Brazil [2 vols.]. Cambridge, MA: Museum of Comparative Zoology (Harvard University).

Pires, J.M., and G.T. Prance. 1985. The vegetation types of the Brazilian Amazon. *In* G.T. Prance and T.E. Lovejoy (editors), Key environments: Amazonia: 109–145. Oxford: Pergamon Press.

Prance, G.T. 1979. Notes on the vegetation of Amazonia III. The terminology of Amazonian forest types subject to inundation. Brittonia 31: 26–38.

Puhakka, M., and R. Kalliola. 1995. Floodplain vegetation mosaics in western Amazonia. Biogeographica 71: 1–14.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. American Naturalist 132: 652–661.

Rambaut, A., A.J. Drummond, D. Xie, G. Baele, and M.A. Suchard. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. Systematic Biology 67: 901–904.

Ratter, J.A., P.W. Richards, G. Argent, and D.R. Gifford. 1973. Observations on the vegetation of northeastern Mato Grosso. I. The woody vegetation types of the Xavantina-Cachimbo expedition area. Philosophical Transactions of the Royal Society of London B 266: 449–492.

Ridgway, R. 1912. Color standards and color nomenclature. Washington, DC: published by the author.

Robinson, G.L., and R.P. Wunderlin. 2005. Revision of *Fevillea* (Cucurbitaceae: Zanonieae). SIDA, Contributions to Botany 21: 1971–1996.

Rocha, R.G., et al. 2015. The Araguaia River as an important biogeographical divide for didelphid marsupials in central Brazil. Journal of Heredity 2015: 593–607.

Ronquist, F., et al. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542.

Rossi, R.V., R.S. Voss, and D.P. Lunde. 2010. A revision of the didelphid marsupial genus *Marmosa*. Part 1. The species in Tate's "Mexicana" and "Mitis" sections and other closely related forms. Bulletin of the American Museum of Natural History 334: 1–83.

Schulenberg, T.S., and K. Awbrey. 1997. A rapid assessment of the humid forests of south-central Chuquisaca, Bolivia (RAP Working Papers 8). Washington, DC: Conservation International.

Siegel, D.C., and S.L. Olson. 2008. The birds of the Republic of Panama. Part 5. Ornithological gazetteer and bibliography. Shipman, VA: Buteo Books.

Silva, L.G.L., D.C. Ferreira, and R.V. Rossi. 2019. Species diversity of *Marmosa* subgenus *Micoureus* (Didelphimorphia, Didelphidae) and taxonomic evaluation of the white-bellied woolly mouse opossum *Marmosa constantiae*. Zoological Journal of the Linnean Society 187: 240–277.

Simmons, N.B., and R.S. Voss. 1998. The mammals of Paracou, French Guiana: a Neotropical lowland rainforest fauna. Part 1. Bats. Bulletin of the American Museum of Natural History 237: 1–219.

Steiner, C., and F.M. Catzeflis. 2004. Genetic variation and geographical structure of five mouse-sized opossums (Marsupialia, Didelphidae) throughout the Guiana Region. Journal of Biogeography 31: 959–973.

Stephens, L., and M.L. Traylor, Jr. 1983. Ornithological gazetteer of Peru. Cambridge, MA: Museum of Comparative Zoology (Harvard University).

Stephens, L., and M.L. Traylor, Jr. 1985. Ornithological gazetteer of the Guianas. Museum of Comparative Zoology (Harvard University).

Sukumaran, J., and L.L. Knowles. 2017. Multispecies coalescent delimits structure, not species. Proceedings of the National Academy of Science 114: 1607–1612.

Tarifa, T., E. Yensen, and F. Guerra. 2008. A preliminary inventory of mammals at a site in the Cordillera Mosetenes, Cochabamba department, Bolivia. Revista Boliviana de Ecología y Conservación Ambiental 24: 73–88.

Tate, G.H.H. 1931. Brief diagnoses of 26 apparently new forms of *Marmosa* (Marsupialia) from South America. American Museum Novitates 493: 1–14.

Tate, G.H.H. 1933. A systematic revision of the marsupial genus *Marmosa* with a discussion of the adaptive radiation of the murine opossums (*Marmosa*). Bulletin of the American Museum of Natural History 66 (1): 1–250 + 26 pls.

Tate, G.H.H. 1939. Mammals of the Guiana Region. Bulletin of the American Museum of Natural History 76 (5): 151–229.

Thomas, O. 1898. Descriptions of new mammals from South America. Annals and Magazine of Natural History (ser. 7) 2: 265–275.

Thomas, O. 1899a. On a new species of *Marmosa*. Annals and Magazine of Natural History (ser. 7) 3: 44–45.

Thomas, O. 1899b. On some small mammals from the district of Cuzco, Peru. Annals and Magazine of Natural History (ser. 7) 3: 40–44.

Thomas, O. 1904a. On the mammals collected by Mr. A. Robert at Chapada, Matto [sic] Grosso (Percy Slader Expedition to Central Brazil). Proceedings of the Zoological Society of London 1903 (2): 232–244, 1 pl.

Thomas, O. 1904b. Two new mammals from South America. Annals and Magazine of Natural History (ser. 7) 13: 142–144.

Thomas, O. 1905. New Neotropical *Chrotopterus, Sciurus, Neacomys, Coendou, Proechimys,* and *Marmosa*. Annals and Magazine of Natural History (ser. 7) 16: 308–314.

Thomas, O. 1920a. A further collection of mammals from Jujuy. Annals and Magazine of Natural History (ser. 9) 5: 188–196.

Thomas, O. 1920b. On mammals from the lower Amazons in the Goeldi Museum, Para. Annals and Magazine of Natural History (ser. 9) 6: 266–283.

Thomas, O. 1924. On a collection of mammals made by Mr. Latham Rutter in the Peruvian Amazon. Annals and Magazine of Natural History (ser. 9) 13: 530–538.

USBGN. 1956. Gazetteer no. 18: Costa Rica. Washington, DC: United States Board on Geographic Names.

USBGN. 1976. Official standard names gazetteer: Nicaragua (2nd ed.). Washington, DC: United States Board on Geographic Names.

Velazco, P.M., and B.D. Patterson. 2019. Small mammals of the Mayo River basin in northern Peru, with the description of a new species of *Sturnira* (Chiroptera: Phyllostomidae). Bulletin of the American Museum of Natural History 429: 1–67.

Vencl, F.V., X. Luan, X. Fu, and L.S. Maroja. 2017. A day-flashing *Photinus* firefly (Coleoptera: Lampyridae) from central Panama: an emergent shift to predator-free space? Insect Systematics and Evolution. [doi: 10.1163/1876312X-48022162]

Vieira, E.M., and E.L.A. Monteiro-Filho. 2003. Vertical stratification of small mammals in the Atlantic rain forest of south-eastern Brazil. Journal of Tropical Ecology 19: 501–507.

Voss, R.S. 1988. Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. Bulletin of the American Museum of Natural History 188 (2): 259–493.

Voss, R.S., and L.H. Emmons. 1996. Mammalian diversity in Neotropical lowland rainforests: a preliminary assessment. Bulletin of the American Museum of Natural History 230: 1–115.

Voss, R.S., and D.W. Fleck. 2011. Mammalian diversity and Matses ethnomammalogy in Amazonian Peru. Part 1. Primates. Bulletin of the American Museum of Natural History 351: 1–81.

Voss, R.S., and S.A. Jansa. 2003. Phylogenetic studies on didelphid marsupials II. Nonmolecular data and new IRBP sequences: separate and combined analyses of didelphine relationships with denser taxon sampling. Bulletin of the American Museum of Natural History 276: 1–82.

Voss, R.S., and S.A. Jansa. 2009. Phylogenetic relationships and classification of didelphid marsupials, an extant radiation of New World metatherian mammals. Bulletin of the American Museum of Natural History 322: 1–177.

Voss, R.S., D.P. Lunde, and N.B. Simmons. 2001. The mammals of Paracou, French Guiana: a Neotropical lowland rainforest fauna. Part 2. Nonvolant species. Bulletin of the American Museum of Natural History 263: 1–236.

Voss, R.S., E.E. Gutiérrez, S. Solari, R.V. Rossi, and S.A. Jansa. 2014. Phylogenetic relationships of mouse opossums (Didelphidae, Marmosa) with a revised subgeneric classification and notes on sympatric diversity. American Museum Novitates 3817: 1–27.

Voss, R.S., J.F. Díaz-Nieto, and S.A. Jansa. 2018. A revision of *Philander* (Marsupialia: Didelphidae), part 1: *P. quica, P. canus*, and a new species from Amazonia. American Museum Novitates 3891: 1–70.

Voss, R.S., D.W. Fleck, and S.A. Jansa. 2019. Mammalian diversity and Matses ethnomammalogy in Amazonian Peru. Part 3: Marsupials (Didelphimorphia). Bulletin of the American Museum of Natural History 432: 1–87.

Wiley, R.H. 2010. Alfonso Olalla and his family: the ornithological exploration of Amazonian Peru. Bulletin of the American Museum of Natural History 343: 1–68.

Woodman, N., et al. 1991. Annotated checklist of the mammals of Cuzco Amazónico, Peru. Occasional Papers of the Museum of Natural History, University of Kansas 145: 1–12.

Woodman, N., N.A. Slade, R.M. Timm, and C.A. Schmidt. 1995. Mammalian community structure in lowland, tropical Peru, as determined by removal trapping. Zoological Journal of the Linnean Society 113: 1–20.

Yablokov, A.V. 1974. Variability of mammals (revised ed.). New Delhi: Amerind Publishing. [Translated from the Russian (original title: Izmenchivost' Mlekopitayushchikh) for the Smithsonian Institution, and edited by L. Van Valen.]

APPENDIX 1

Gazetteer of Sequenced Specimens of *Marmosa* (*Micoureus*)

Below we list all the localities where sequenced specimens of the subgenus *Micoureus* were collected, including those sequenced by us and others corresponding to sequences we downloaded from GenBank (table 2). Italicized place names are those of the largest political units within each country (states, departments, provinces, etc.). Geographic coordinates (in decimal degrees) were obtained from primary sources (e.g., specimen labels; in parentheses) or secondary sources (institutional databases or publications, cited in square brackets). Numbers identify locality symbols plotted on maps in Materials and Methods (figs. 1–3).

BOLIVIA

1. *Beni,* Río Iténez frente Costa Marquez [12.48°S, 64.28°W; Anderson, 1997].
2. *Chuquisaca,* El Limón, 15.6 km N El Palmar (20.71°S, 64.31°W).
3. *Chuquisaca,* Rinconada del Bufete [= Cerro Bufete at 20.83°S, 64.38°W; Patton et al., 2015].
4. *Chuquisaca,* Río Limón (19.55°S, 64.13°W).
5. *Cochabamba,* 4.4 km by road N Tablas Monte [17.07°S, 65.98°W; Anderson, 1997].
6. *Cochabamba,* Chapare, Serranía Mosetenes [16.23°S, 66.42°W; Tarifa et al., 2008].
7. *La Paz,* 1 mi W Puerto Linares [15.48°S, 67.52°W; Anderson, 1997].
8. *La Paz,* La Reserva [15.73°S, 67.52°W; Anderson, 1997].
9. *Pando,* La Cruz (11.45°S, 67.22°W).
10. *Santa Cruz,* 1 km NE Estancia Cuevas (18.18°S, 63.73°W).
11. *Santa Cruz,* 27 km SE Santa Cruz (17.97°S, 63.05°W).
12. *Santa Cruz,* 53 km E Boyuibe [20.45°S, 62.83°W; Anderson, 1997].
13. *Santa Cruz,* Parque Nacional Noel Kempff Mercado, El Refugio (14.77°S, 61.03°W).
14. *Santa Cruz,* Parque Nacional Noel Kempff Mercado, Flor de Oro [13.55°S, 61.01°W; USNM database].
15. *Tarija,* 5 km NNW Entre Ríos (21.48°S, 64.20°W).

BRAZIL

16. *Acre,* Igarapé Porongaba, right bank Rio Juruá (8.67°S, 72.78°W).
17. *Alagoas,* São José de Lajes [8.96°S, 36.07°W; Rocha et al., 2015].
18. *Amazonas,* alto Rio Urucu [4.85°S, 65.27°W; MVZ database].
19. *Amazonas,* Barcelos [0.06°S, 64.59°W; F.C. Almeida, personal commun.].
20. *Amazonas,* Barro Vermelho, left bank Rio Juruá [6.47°S, 68.77°W; Patton et al., 2000].
21. *Amazonas,* Comunidade Colina, right bank Rio Tiquié [0.12°N, 69.01°W; Patton et al., 2015].
22. *Amazonas,* Igarapé Nova Empresa, left bank Rio Juruá (6.80°S, 70.73°W).
23. *Amazonas,* Penedo, right bank Rio Juruá [6.83°S, 70.75°W; Patton et al., 2000].
24. *Amazonas,* Santa Isabel do Rio Negro [0.76°S, 63.44°W; F.C. Almeida, personal commun.].
25. *Amazonas,* Seringal Condor, left bank Rio Juruá [6.75°S, 70.85°W; Patton et al., 2000].
26. *Amazonas,* Villa Bella Imperatriz, Boca Rio Andira [2.75°S, 56.82°W; Paynter and Traylor, 1991].
27. *Bahia,* Fazenda Bolandeira, 10 km S Una [15.35°S, 39.00°W; MVZ database].
28. *Bahia,* Fazenda Santa Rita, 8 km E Andaraí [12.80°S, 41.27°W; Costa et al., 2003].
29. *Bahia,* Itacaré, Fazenda Rio Capitão [14.34°S, 39.09°W; F.C. Almeida, personal commun.].
30. *Bahia,* Itamari, Fazenda Alto São Roque [13.85°S, 39.67°W; F.C. Almeida, personal commun.].
31. *Bahia,* Nova Viçosa [17.81°S, 39.66°W; Rocha et al., 2015].
32. *Bahia,* Porto Seguro, Parque Nacional do Pau Brasil [16.52°S, 39.30°W; F.C. Almeida, personal commun.].
33. *Bahia,* Uruçuca, Fazenda Caititu [14.42°S, 39.07°W; F.C. Almeida, personal commun.].

34. *Ceará,* locality unknown [3.71°S, 38.50°W at Fortaleza, the state capital; Paynter and Traylor, 1991].
35. *Goiás,* Mimoso de Goiás [15.06°S, 48.19°W; F.C. Almeida, personal commun.].
36. *Mato Grosso,* Chapada dos Guimarães, Usina Hidrelétrica Manso [15.58°S, 56.10°W; Bonvicino et al., 2002].
37. *Mato Grosso,* Fazenda Lagoa Bonita, 36 km N Barra do Garças [15.58°S, 52.36°W; MVZ database].
38. *Mato Grosso,* Fazenda Noirumbá, 34 km NW Riberão Cascalheira [12.64°S, 51.93°W; MVZ database].
39. *Mato Grosso,* 40 km N Alta Floresta (including sublocalities "left bank Rio Cristalino" and "Reserva Ecológica Cristalino") [9.60°S, 55.93°W; MVZ database].
40. *Mato Grosso,* São José do Xingu [10.80°S, 52.74°W; F.C. Almeida, personal commun.].
41. *Mato Grosso do Sul,* Corumbá, São Marcus road, 10 km NE Urucum [19.10°S, 57.58°W; Gardner, 2008].
42. *Minas Gerais,* 13 km E Marliéria [19.72°S, 42.65°W; MVZ database].
43. *Minas Gerais,* Berilo, Usina Hidrelétrica de Irapé [16.74°S, 42.59°W; F.C. Almeida, personal commun.].
44. *Minas Gerais,* Casa Branca, Parque Estadual Rola Moça [20.12°S, 44.12°W; F.C. Almeida, personal commun.].
45. *Minas Gerais,* Estação Ecológica de Acauã, 17 km N Turmalina [17.17°S, 42.78°W; Carrara et al., 2013].
46. *Minas Gerais,* Marliéria, Parque Estadual do Rio Doce (including sublocalities "Campolina" and "Vinhático") [19.76°S, 42.63°W; F.C. Almeida, personal commun.].
47. *Pará,* 52 km SSW Altamira, east bank Rio Xingu (3.65°S, 52.37°W).
48. *Pará,* BR165 Santarém-Cuiabá, km 217 [4.00°S, 54.67°W; Patton et al., 2015].
49. *Pará,* Canaã dos Carajás [6.38°S, 50.38°W; Rocha et al., 2015].
50. *Pará,* Goanésia do Pará [3.71°S, 48.62°W; Rocha et al., 2015].
51. *Pará,* Kayapó Indigenous Area, Pinkaití Research Station (7.77°S, 51.97°W).
52. *Pará,* Novo Repartimento [4.11°S, 50.09°W; Rocha et al., 2015].
53. *Pará,* Santana do Araguaia [9.63°S, 50.14°W; Rocha et al., 2015].
54. *Rio de Janeiro,* Guapimirim [22.54°S, 42.98°W; F.C. Almeida, personal commun.].
55. *São Paulo,* Fazenda Intervales, Base do Carmo, 5.5 km S Capão Bonito, 700 m (24.33°S, 48.42°W).
56. *São Paulo,* Sorocaba, Floresta Nacional de Ipanema [23.44°S, 47.63°W; Patton et al., 2015].
57. *Tocantins,* Caseara [9.30°S, 49.96°W; Rocha et al., 2015].
58. *Tocantins,* N Pium [9.47°S, 50.09°W; Rocha et al., 2015].
59. *Tocantins,* S Pium [9.98°S, 50.03°W; Rocha et al., 2015].

COLOMBIA

60. *Antioquia,* Corregimiento El Cedro, Vereda Corcovado, Finca El Bosque, Bosque San Andres (7.07°N, 75.42°W).
61. *Antioquia,* San Jerónimo, NW Medellín, 420 m [6.45°N, 75.75°W; Paynter, 1997].
62. *Antioquia,* Sonsón, 9 km E Río Negrito, 2050 m [5.70°N, 75.30°W; Patton et al., 2015].
63. *Caquetá,* Río Caquetá, Tres Troncos [0.13°N, 74.68°W; Patton et al., 2015].
64. *Cauca,* Chisquio, 1700 m [2.48°N, 76.87°W; Paynter, 1997].
65. *Cesar,* Sierra Negra, Villanueva [10.60°N, 72.92°W; Patton et al., 2015].
66. *Chocó,* Río Baudó, Río Sandó [5.05°N, 76.95°W; Paynter, 1997].
67. *Huila,* Acevedo, San Adolfo, 1400 m [1.62°N, 75.98°W; Paynter, 1997].
68. *Huila,* San Augustín, [Río] San Antonio, 2300 m [1.95°N, 76.48°W; Paynter, 1997].
69. *Huila,* San Augustín, Río Majuas, 2800 m [1.95°N, 76.40°W; Apanaskevich et al., 2017].

COSTA RICA

70. *Cartago,* Agua Caliente [9.85°N, 83.93°W; VertNet database].

71. *Puntarenas,* Monteverde [10.25°N, 84.77°W; Clark et al., 2000].
72. *San José,* San José [9.93°N, 84.08°W; USBGN, 1956].

ECUADOR

73. *Esmeraldas,* Esmeraldas [0.98°N, 79.70°W; Paynter, 1993].
74. *Loja,* 12 km E (by road) Portovelo [3.72°S, 79.55°W; Paynter, 1993].
75. *Orellana,* 42 km S and 1 km E Pompeya Sur (0.68°S, 76.43°W).
76. *Orellana,* Parque Nacional Yasuní, 35 km S Pompeya Sur (0.63°S, 76.47°W).

FRENCH GUIANA (FRANCE)

77. Camp du Tigre [4.91°N, 52.31°W; Jiménez et al., 2011].
78. Les Nouragues [4.08°N, 52.67°W; Voss and Emmons, 1996].
79. Paracou [5.28°N, 52.92°W; Simmons and Voss, 1998].
80. Pic Matecho [3.75°N, 53.03°W; Byles et al., 2013].
81. Saül [3.62°N, 53.22°W; Byles et al., 2013].

GUYANA

82. *Potaro-Siparuni,* Iwokrama Reserve, 25 km SSW Kurupukari [4.28°N, 58.47°W; ROM database].
83. *Potaro-Siparuni,* Iwokrama Reserve, 5 km SW Kurupukari (4.63°N, 58.72°W).
84. *Upper Demerara-Berbice,* West Pibiri (5.03°N, 58.63°W).
85. *Upper Takutu-Upper Essequibo,* Chodikar River, 55 km SW Gunn's Strip (1.37°N, 58.77°W).
86. *Upper Takutu-Upper Essequibo,* Quarter Mile Landing, Rupununi River, 5 km S Arrai [3.92°N, 59.10°W; ROM database].

NICARAGUA

87. *Zelaya,* Río Siquía [presumably the stream near Rama at 12.15°N, 84.22°W; USBGN, 1976].

PANAMA

88. *Bocas del Toro,* Isla San Cristobal, Bocatorito [9.23°N, 82.27°W; Siegel and Olson, 2008].
89. *Colón,* Parque Nacional Soberanía, Pipeline Road, 1 km N Río Mendoza [9.17°N, 79.75°W; Vencl et al., 2017].

PARAGUAY

90. *Amambay,* 33 km SE Pedro Juan Caballero, Parque Nacional Cerro Corá [22.67°S, 55.98°W; Paynter, 1989].
91. *Canindeyú,* Reserva Morombí [24.72°S, 55.43°W; de la Sancha et al., 2012].
92. *Itapúa,* Reserva San Rafael [26.57°S, 55.68°W; de la Sancha et al., 2012].
93. *San Pedro,* Ganadera La Carolina (24.09°S, 56.41°W).

PERU

94. *Amazonas,* Huampami, Río Cenepa (4.47°S, 78.17°W).
95. *Cajamarca,* San Ignacio, Tabaconas, Cerro La Viuda (5.28°S, 79.32°W).
96. *Cuzco,* 2 km SSW Tangoshiari, 530 m (11.77°S, 73.33°W).
97. *Cuzco,* Paucartambo, Consuelo, 15.9 km SW Pilcopata, 1000 m [13.02°S, 71.49°W; FMNH database].
98. *Cuzco,* Ridge Camp, 1000 m (11.78°S, 73.33°W).
99. *Cuzco,* Vilcanota River just north of Cuzco [13.12°S, 72.65°W; Ceballos-Bendezú, 1982].
100. *Huánuco,* Río Cayumba, Hacienda Porvenir [9.43°S, 76.00°W; Stephens and Traylor, 1983].
101. *Junín,* "Camp 2" in Cordillera Vilcabamba (11.55°S, 73.63°W).
102. *Loreto,* 1.5 km N Teniente López [2.60°S, 76.12°W; Duellman and Mendelson, 1995].
103. *Loreto,* 25 km S Iquitos, Estación Biológica Allpahuayo [3.97°S, 73.42°W; Hice and Velazco, 2012].
104. *Loreto,* Quebrada Orán, ca. 5 km N Río Amazonas [3.48°S, 72.52°W; Patton et al., 2015].
105. *Loreto,* Río Gálvez, Nuevo San Juan [5.25°S, 73.17°W; Voss and Fleck, 2011].
106. *Loreto,* San Jacinto [2.32°S, 74.87°W; Duellman and Mendelson, 1995].
107. *Loreto,* Teniente López [2.60°S, 76.12°W; Duellman and Mendelson, 1995].

108. *Madre de Dios,* 15 km E Puerto Maldonado, Reserva Cuzco Amazónico [12.58°S, 69.08°W; Duellman and Koechlin, 1991].
109. *San Martín,* Moyobamba, Wagonki, Área de Conservación Municipal Mishquiyacu-Rumiyacu y Almendra, 1000 m [= Waqanki at 6.08°S, 76.98°W, 970 m; Velazco and Patterson, 2019].

VENEZUELA

110. *Amazonas,* Cerro Neblina Camp V [0.83°N, 65.98°W; USNM database].
111. *Amazonas,* Cerro Neblina Camp VII [0.84°N, 65.97°W; Patton et al., 2015].
112. *Amazonas,* Cerro Neblina Camp XI [0.87°N, 65.97°W; Patton et al., 2015].
113. *Aragua,* Estación Biológica de Rancho Grande [10.37°N, 67.68°W; Patton et al., 2015].
114. *Bolívar,* 126 km SW Río Cuyuní, 1400 m [5.68°N, 61.32°W; MVZ database].
115. *Falcón,* Serranía de San Luis, 9 km N Cabure [11.23°N, 69.61°W; Patton et al., 2015].

APPENDIX 2

PRIMERS USED TO AMPLIFY CYTB FROM DEGRADED DNA

Primer name	Primer sequence
CYTB-F1-Didelphidae	5′ ATAACCTATGGCATGAAAAACCATTGTTG
CYTB-R1-Didelphidae	5′ CCTTCATTGCTGGCTTACAAGGC
CYTB-420R-Didelphidae	5′ GCTCCTCAGAAGGATATTTGTCCTCA
CYTB-730R-*Marmosa*	5′ TCWCCTAATARRTCWGGTGARAATATTGC
CYTB-540F-*Marmosa*	5′ GAGGAGGMTTYTCHGTTGATAAAGC
CYTB-650F-*Marmosa*	5′ CTATTCCTTCACGAAACAGGCTC
CYTB-217R-*Marmosa*	5′ TCTGTAGCCCAYATYTGYCGWGAYG
CYTB-70F-*Marmosa*	5′ CCMTCAAATATTTCAGCCTGATG
CYTB-365R-*Micoureus*	5′ CAGTAAGTAGAAGRATAACTCC
CYTB-495R-*Micoureus*	5′ CCTCARATTCATTCAACTAATG
CYTB-220F-*Micoureus*	5′ TTAACAGCATTYTCATCTGTAGC

APPENDIX 3

Gazetteer of Examined Specimens of the Rapposa Group

This gazetteer includes all localities from which we personally examined specimens of the Rapposa Group of the subgenus *Micoureus*. Italicized place names are those of currently recognized departments, provinces, or states; boldface identifies collection localities as they appear in the text of this report. Unless recorded by the collector, geographic coordinates and elevation above sea level are provided in square brackets with a cited secondary source for these data. The name(s) of species collected at each locality are separated from the locality name and geographic data by a colon, followed by the name(s) of the collector(s) and date(s) of collection in parentheses. Numbers identify locality symbols plotted on maps that accompany the species accounts in our text (figs. 12, 17).

ARGENTINA

1. *Jujuy,* Río San Francisco, **Altura de Yuto** [23.63°S, 64.47°W; Gardner, 2008], 500 m: *Marmosa rapposa* (E. Budin, 23 July 1919).

BOLIVIA

2. *Beni,* **5 km N Estancia El Porvenir,** Isla de Bosque (14.51°S, 66.35°W), 201 m: *Marmosa rapposa* (J. Salazar, 10 August 1988).
3. *Chuquisaca,* **2 km E Chuyayacu** (19.72°S, 63.85°W), 1200 m: *Marmosa rapposa* (E. Palma, 9 August 1990).
4. *Chuquisaca,* **El Limón** (20.72°S, 64.32°W), left bank Río Santa Marta, 15.6 km N El Palmar, 900 m: *Marmosa rapposa* (L.H. Emmons, 26 May 1995).
5. *Chuquisaca,* **Rinconada del Bufete** [20.83°S, 64.37°W; Schulenberg and Awbrey, 1997], 2050 m: *Marmosa rapposa* (L.H. Emmons, 19 May 1995).
6. *Chuquisaca,* **Río Limón** (19.55°S, 64.13°W), 1300 m: *Marmosa rapposa* (R.L. Cuéllar, 3 August 1990).
7. *Cochabamba,* **Serranía Mosetenes** [16.23°S, 66.42°W; Tarifa et al., 2008]: *Marmosa rapposa* (F. Guerra, 6–7 September 2003).
8. *Cochabamba,* **4.4 km by road N Tablas Monte,** Río Jatun Mayu (17.07°S, 66.00°W), 1833 m: *Marmosa rapposa* (J.L. Dunnum, 13–16 July 1993; S.C. Peurach, 14 July 1993).
9. *Cochabamba,* **9.5 km NE Tablas Monte,** Río Jatun Mayu (17.03°S, 65.98°W), 1500 m: *Marmosa rapposa* (J.L. Dunnum, 17 July 1993; C.T. Seaton, 16 July 1993; J. Peralta, 16 July 1993).
10. *La Paz,* **4 km NW Alcoche** [15.67°S, 67.70°W, 425 m; Anderson, 1997]: *Marmosa rapposa* (G.K. Creighton, 10–11 May 1978).
11. *La Paz,* **20 km NNE Caranavi** [15.70°S, 67.58°W, 2000 ft; Anderson, 1997]: *Marmosa rapposa* (G.K. Creighton, 6–7 May 1978).
12. *La Paz,* **Cajuata** [16.82°S, 67.25°W, ca. 1800 m; Paynter, 1992]: *Marmosa rapposa* (collector and dates unknown).
13. *La Paz,* **La Reserva** (15.73°S, 67.52°W), 840–950 m: *Marmosa rapposa* (AMNH/MSB expedition, 24–29 July 1992, 18–22 May 1996).
14. *La Paz,* **1 km S La Reserva** [15.75°S, 67.52°W; Anderson, 1997), 1100 m: *Marmosa rapposa* (R.J. Vargas, 21 September 1992; E. Yensen, 20 September 1992).
15. *La Paz,* **Los Molinos de Titiamaya** [ca. 16.92°S, 67.19°W; Mapcarta website], 2744 m: *Marmosa rapposa* (S.F. Moolenijzer, 1 August 1993).
16. *La Paz,* **Ñequejahuira** [ca. 16.33°S, 67.83°W; Paynter, 1992], 8000 ft: *Marmosa rapposa* (G.H.H. Tate, 23 May 1926).
17. *La Paz,* **1 mi W Puerto Linares** [15.48°S, 67.52°W, ca. 500 m; Anderson, 1997]: *Marmosa rapposa* (W.D. Webster, 23 July 1979).
18. *Santa Cruz,* **53 km E Boyuibe** (20.45°S, 62.83°W), 600 m; *Marmosa rapposa* (E. Palma, 6 July 1991).
19. *Santa Cruz,* **Buenavista** [17.45°S, 63.67°W; Anderson, 1997], 500 m: *Marmosa rapposa* (F. Steinbach, 1926–1929; J. Steinbach, 1920–1924).

20. *Santa Cruz,* **Cerro Hosane** [17.42°S, 64.00°W; Dirksen and De la Riva, 1999], 1300 m: *Marmosa rapposa* (J. Steinbach, 13–18 August 1917).
21. *Santa Cruz,* **2 km N Chapare River mouth** [15.95°S, 64.68°W; Anderson, 1997]: *Marmosa rapposa* (D.E. Añez, 31 July 1965; A. Ximénez, 28 July 1965).
22. *Santa Cruz,* **ca. 54 km S Chapare River mouth** [16.48°S, 64.73°W; Anderson, 1997]: *Marmosa rapposa* (A. Ximénez, 22 July 1965).
23. *Santa Cruz,* **1 km NE Estancia Cuevas** (18.18°S, 63.73°W), 1300 m: *Marmosa rapposa* (J.L. Dunnum, 25 May 1991).
24. *Santa Cruz,* **27 km SE Santa Cruz** (17.97°S, 63.05°W), 365 m: *Marmosa rapposa* (B.J. Hayward, 29 May 1988).
25. *Santa Cruz,* **Warnes** [17.50°S, 63.17°W; Paynter, 1992]: *Marmosa rapposa* (R. Villalobos, 15 August 1966).
26. *Tarija,* **3 km WNW Carapari** (21.80°S, 63.78°W), 850 m: *Marmosa rapposa* (S. Anderson, 16 August 1991)
27. *Tarija,* **5 km NNW Entre Ríos** (21.48°S, 64.20°W), 1600 m: *Marmosa rapposa* (E. Peñaranda, 12 August 1991).

BRAZIL

28. *Acre,* **Igarapé Porongaba,** right bank Rio Juruá [8.67°S, 72.78°W; Patton et al., 2000]: *Marmosa rutteri* (M.N.F. da Silva, 22 February 1992).
29. *Acre,* **Nova Vida,** right bank Rio Juruá [8.37°S, 72.82°W; Patton et al., 2000]: *Marmosa rutteri* (M.N.F. da Silva, 13 March 1992).
30. *Amazonas,* **Boa Esperança,** right bank Rio Juruá [6.53°S, 68.92°W; Patton et al., 2000]: *Marmosa rutteri* (J.L. Patton, 13 November 1991).
31. *Amazonas,* **Igarapé Nova Empressa,** left bank Rio Juruá [6.80°S, 70.73°W; Patton et al., 2000]: *Marmosa rutteri* (J.L. Patton, 31 August–3 September 1991).
32. *Amazonas,* **opposite Altamira,** left bank Rio Juruá [6.58°S, 68.93°W; Patton et al., 2000]: *Marmosa rutteri* (J.L. Patton, 13 November 1991).
33. *Amazonas,* **Penedo,** right bank Rio Juruá [6.83°S, 70.75°W; Patton et al., 2000]: J.L. Patton, 29 August–7 September 1991).
34. *Mato Grosso,* **264 km N Xavantina** (12.85°S, 51.77°W, ca. 1750 ft): *Marmosa rapposa* (R.L. Jackson, 22 July 1968).
35. *Mato Grosso do Sul,* Corumbá, São Marcos Road, **10 km NE Urucum** [19.10°S, 57.58°W; Gardner, 2008]: *Marmosa rapposa* (M.L. Kuns, 15 September 1965).

COLOMBIA

36. *Amazonas,* **Leticia** [4.15°S, 69.95°W, ca. 100 m; Paynter, 1997): *Marmosa rutteri* (R.H. Rageot, March 1979).
37. *Caquetá,* **Tres Troncos** [0.13°N, 74.68°W; Hershkovitz, 1977], 185 m: *Marmosa rutteri* (P. Hershkovitz, 27 January–1 February 1952).

ECUADOR

38. *Napo,* "near the river Napo" [0.98°S, 77.82°W; Voss, 1988], 2400–3000 feet: *Marmosa rutteri* (L. Söderström, June 1921–January 1923). Probably near Tena, which is close to where the old trail from Baeza to Puyo crossed the Napo.
39. *Orellana,* **San José de Payamino** [0.50°S, 77.28°W; Paynter, 1993], 300 m: *Marmosa rutteri* (R.M. Timm, 25 January 1984).
40. *Sucumbíos,* **Boca Lagarto Cocha** [= Boca Río Lagartococha at 0.65°S, 75.27°W; Paynter, 1993]: *Marmosa rutteri* (Olalla y Hijos, 15–16 January 1926). Misspelled "Voca Lagarto Cocha" on the original skin tags, this locality is on the Ecuadorean-Peruvian frontier, which is formed by the Río Lagartococha. As discussed by Wiley (2010: 37–38), it is not actually known whether specimens from this locality were collected on the Ecuadorean or the Peruvian side of the river.

PARAGUAY

41. *Alto Paraguay,* **Puerto Casado** [22.33°S, 57.92°W; Paynter, 1989], 150 m: *Marmosa rapposa* (P. Willim, 6 July 1960).

42. *Amambay,* **Parque Nacional Cerro Corá** [ca. 22.67°S, 55.98°W; Paynter, 1989]: *Marmosa rapposa* (E. Palma at "33 km SE Pedro Juan Caballero," 26 May 1991; G.K. Creighton, 1979).
43. *San Pedro,* **Ganadera La Carolina** (24.09°S, 56.41°W): *Marmosa rapposa* (G. D'Elía, 29–31 March 2001).

PERU

44. *Amazonas,* **La Poza** [4.02°S, 77.77°W, 170 m; Patton et al., 1982] on Río Santiago: *Marmosa rutteri* (J.L. Patton, 17–24 August 1979).
45. *Amazonas,* **mouth of Río Cenepa** [4.58°S, 78.20°W; Stephens and Traylor, 1983]: *Marmosa rutteri* (J.M. Schunke, 24 October 1929). The original collector's skin tag on AMNH 98712 gives this locality as "Mündung Cenipa Fluss."
46. *Amazonas,* **vicinity of Huampami,** Río Cenepa, 700 ft [4.47°S, 78.17°W, 210 m; Patton et al., 1982]: *Marmosa rutteri* (J.L. Patton, 9 July 1977, 10 July–11 August 1978).
47. *Amazonas,* **vicinity of Kayamas** [4.45°S, 78.17°W; MVZ database], Río Cenepa: *Marmosa rutteri* (J.L. Patton, 2 August 1977).
48. *Ayacucho,* **Santa Rosa on Río Santa Rosa** (12.70°S, 73.72°W), ca. 800 m: *Marmosa rutteri* (J.P. O'Neill, 11 July 1970). The collector's skin tag gives the longitude as 76°43′W, an obvious lapsus: the department of Ayacucho does not extend to 76°W, and Santa Rosa is known to be near Luisiana (ca. 12.65°S, 73.73°W; Stephens and Traylor, 1983) on the Río Apurimac.
49. *Cuzco,* **Hacienda Cadena** [13.40°S, 70.72°W; Stephens and Traylor, 1983], 1000 m: *Marmosa rapposa* (C. Kalinowski, 22 December 1948, 25 November 1949).
50. *Cuzco,* La Convención, Kimbiri, **Llactahuamán** [ca. 12.87°S, 73.52°W; Gardner, 2008], 1710 m: *Marmosa rapposa* (E. Vivar, 25 June 1998).
51. *Cuzco,* **Quincemil** [13.27°S, 70.63°W; Stephens and Traylor, 1983], 680 m: *Marmosa rapposa* (C. Kalinowski, 8 August 1953).
52. *Cuzco,* **Vilcanota River just north of Cuzco** [probably near Huadquiña at 13.12°S, 72.65°W; Stephens and Traylor, 1983], 1500 m: type locality of *Marmosa rapposa* (O. Garlepp, December 1897). This locality was recorded as "Vilcanota nordl[lich]. v[on]. Cuzco, Peru, 1500 m" on original labels still attached to the paratypes.
53. *Huánuco,* **Chinchavita** [= Chinchavito, at 9.48°S, 75.92°W, ca. 1000 m; Stephens and Traylor, 1983]: *Marmosa parda* (R.W. Hendee, 26–29 December 1926).
54. *Huánuco,* **Huachipa** [ca. 9.50°S, 75.87°W, 855–1405 m; Stephens and Traylor, 1983]: *Marmosa parda* (J.T. Zimmer, 28 September 1922).
55. *Huánuco,* Río Cayumba, **Hacienda Porvenir** [ca. 6 km above Hacienda Éxito at 9.43°S, 76.00°W; Stephens and Traylor, 1983], 3000 ft: *Marmosa parda* (E. Heller, 18 August 1922).
56. *Huánuco,* Río Chinchao, **Hacienda San Antonio** [ca. 9.55°S, 75.87°W; Stephens and Traylor, 1983], 3000 ft: *Marmosa parda* (E. Heller, 3–19 September 1922).
57. *Junín,* **"Camp Two" in Cordillera Vilcabamba** (11.55°S, 73.63°W, 2050 m): *Marmosa rapposa* (L.H. Emmons, 28 June–1 July 1997; L. Luna W., 1 July 1997). "Camp Two" is the name assigned by Alonso et al. (2001) to the site with these coordinates visited by Conservation International's Rapid Assessment Program (CI-RAP) expedition in 1997. Expedition personnel did not use this place name on specimen tags or in field notes, which only identified this camp by its coordinates and elevation.
58. *Junín,* **Utcuyacu** [ca. 11.20°S, 75.47°W, 1400–1465 m; Stephens and Traylor, 1983], including nearby sublocality **15 km by road SW San Ramón** (1400 m): *Marmosa rapposa* (H. Watkins, 25 November–6 December 1919; G.K. Creighton, 19–20 May 1980).
59. *La Libertad,* Utcubamba, **on trail to Ongón** [ca. 8.27°S, 76.97°W; Stephens and Traylor, 1983], 1825 m: *Marmosa parda* (L.J. Barkey, 30 October 1979).

60. *Loreto,* **Boca Río Curaray** [2.37°S, 74.08°W; Wiley, 2010]: *Marmosa rutteri* (Olalla y Hijos, 29 October 1925–16 January 1926). See Wiley (2010: 34–37) for a discussion of this locality, which the Olallas consistently misspelled "Voca R. Curaray," and which has often been misinterpreted as being in Ecuador.
61. *Loreto,* **Nuevo San Juan** [5.25°S, 73.17°W; Voss and Fleck, 2011], Río Gálvez: *Marmosa rutteri* (D.W. Fleck, 25 June 1995, 10 July 1996, 21–27 October 1999).
62. *Loreto,* **Orosa** [ca. 3.53°S, 72.18°W; Wiley, 2010], Río Amazonas: *Marmosa rutteri* (Olalla y Hijos, 26 October 1926).
63. *Loreto,* **Otorongo** [= Fuerte Militar Otorongo at 3.95°S, 73.37°W; Hice and Velazco, 2012], "km 21 carretera Iquitos-Nauta," 120 m: *Marmosa rutteri* (W. Sánchez, 14 August 2003).
64. *Loreto,* Iquitos, **Pampa Chica** [ca. 3.75°S, 73.20°W, 106 m; Stephens and Traylor, 1983]: *Marmosa rutteri* (C. Kalinowski, 29 August 1956). On modern maps "Pampachica" is shown as a suburb of Iquitos; in Kalinowski's day it was probably a village just outside the city, whose coordinates and elevation are used as approximations for this locality.
65. Loreto, Iquitos, **"Triunfo Chacras"** [ca. 4.15°S, 73.47°W; Hurtado et al., 2014]: *Marmosa rutteri* (C.L. Hice, 4 February 2003). The locality name presumably refers to agricultural fields (*chacras*) near El Triunfo, a small community about 48 km SW of Iquitos on the road to Nauta.
66. *Loreto,* Río Itaya, **San Antonio** [4.17°S, 73.33°W, 150 m; Robinson and Wunderlin, 2005]: *Marmosa rutteri* (J.M. Schunke, 25 October 1927).
67. *Loreto,* **San Jerónimo,** 1000 ft [7.92°S, 74.91°W; Patton et al., 2015]: *Marmosa rutteri* (R.W. Hendee, 29 November–10 December 1927).
68. *Loreto,* **Sarayacu** [6.73°S, 75.10°W, 125 m; Stephens and Traylor, 1983], Río Ucayali: *Marmosa rutteri* (Olalla y Hijos, 2–27 April 1927).
69. *Loreto,* **Yurimaguas** [5.90°S, 76.08°W, 182 m; Stephens and Traylor, 1983]: *Marmosa rutteri* (M.P. Anderson, 17 September 1912).
70. *Madre de Dios,* **Blanquillo** [12.43°S, 70.70°W, 273 m; S. Solari, personal commun.]: *Marmosa rutteri* (S. Solari, 22 February 1993).
71. *Madre de Dios,* 15 km E Puerto Maldonado, **Reserva Cuzco Amazónico** [12.55°S, 69.05°W, ca 200 m; Duellman and Koechlin, 1991]: *Marmosa rutteri* (C.A. Schmidt, R.M. Timm, and N. Woodman; 1989–1990).
72. *Pasco,* Oxapampa, **San Pablo** (ca. 10.45°S, 74.87°W; Stephens and Traylor, 1983), 900 ft: *Marmosa rutteri* (Andrews University field crew, 5–13 July 1964).
73. *Puno,* **11 km NNE Ollachea** [13.72°S, 70.44°W; MVZ collection database], 1880 m: *Marmosa rapposa* (J.L. Patton, 10–13 July 1986).
74. *Puno,* **14 km W Yanahuaya** [14.27°S, 69.33°W; MVZ collection database], 2210 m: *Marmosa rapposa* (J.L. Patton, 28 July 1986).
75. *Ucayali,* **Tushemo** [8.60°S, 74.32°W, 225 m; Gardner, 2008], near Masisea: *Marmosa rutteri* (L. Rutter, 10 September 1923).
76. *Ucayali,* Río Ucayali, **Yarinacocha** [8.25°S, 74.72°W, ca. 100 m; Stephens and Traylor, 1983]: *Marmosa rutteri* (J.M. Schunke, 5 June 1945).

Scientific Publications of the American Museum of Natural History

American Museum Novitates
Bulletin of the American Museum of Natural History
Anthropological Papers of the American Museum of Natural History

Publications Committee
Robert S. Voss, Chair

Board of Editors
Jin Meng, Paleontology
Lorenzo Prendini, Invertebrate Zoology
Robert S. Voss, Vertebrate Zoology
Peter M. Whiteley, Anthropology

Managing Editor
Mary Knight

Submission procedures can be found at http://research.amnh.org/scipubs

All issues of *Novitates* and *Bulletin* are available on the web (http://digitallibrary.amnh.org/dspace). Order printed copies on the web from:
http://shop.amnh.org/a701/shop-by-category/books/scientific-publications.html

or via standard mail from:
American Museum of Natural History—Scientific Publications
Central Park West at 79th Street
New York, NY 10024

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).

On the cover: Holotype skull of *Marmosa rapposa* Thomas, 1899, an adult female specimen collected by Otto Garlepp in Cuzco department, Peru (BMNH 98.11.6.13).